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dissertation entitled

HIERARCHICAL BAYESIAN THRESHOLD MODELS APPLIED TO THE
QUANTITATIVE GENETIC ANALYSIS OF CALVING EASE SCORES
IN ITALIAN PIEMONTESE CATTLE

presented by

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has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Animal Science

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Date 8/13/02

DATE DUE	DATE DUE	DATE DUE

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By

Kadir Kizilkaya

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Animal Science

2002

ABSTRACT

HIERARCHICAL BAYESIAN THRESHOLD MODELS APPLIED TO THE QUANTITATIVE GENETIC ANALYSIS OF CALVING EASE SCORES IN ITALIAN PIEMONTESE CATTLE

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First parity calving ease scores for Italian Piemontese cattle were analyzed using sire and maternal grandsire threshold models. Genetic parameters were estimated by approximate marginal maximum likelihood (MML) methods such as the historically popular expectation-maximization method and Laplace's method in addition to inferentially exact Markov Chain Monte Carlo (MCMC) methods. Laplacian MML and MCMC point estimates of variance components and direct and maternal heritabilities were seen to be statistically significant with measures of uncertainty that were virtually identical to each other. Furthermore, the joint modal estimates of sire effects and associated standard errors conditioned on MML estimates of variance and covariance components were seen to differ little from the respective posterior means and standard deviations derived from MCMC. These results suggest that there may be little need to consider computationally intensive MCMC methods for national breed genetic evaluations derived from large calving ease datasets in cattle production industries.

A heavier tailed Student *t* residual distribution may be specified as an alternative to the normal distribution for modeling underlying liability variables that characterize a threshold probit-link model. Both *t*-link and probit link models were applied to simulated

data sets characterized by various degrees of freedom specifications for *t*-error on the liability variables. Model choice, using either the deviance information criteria (DIC) or the log marginal likelihood (LML), was generally correctly assigned in all cases, whether for the direct linear model analysis of liability variables or for the threshold model analysis of the corresponding ordinal data. The threshold *t*-link sire maternal-grandsire model was found to better fit Italian Piemontese calving ease data compared to the regular threshold cumulative probit link model; nevertheless, the rank correlation on posterior means of breeding values between a threshold-*t* and regular threshold model analyses exceeded 0.98.

A hierarchical generalized linear mixed model based on a structural multifactorial model with fixed and random effects that multiplicatively influence residual heteroskedasticity was developed. Validation of models and MCMC algorithms were based on simulated normal and ordinal categorical data with heteroskedastic residual structures. Simulation results indicated that DIC and LML were useful in correctly choosing between heteroskedastic and homoskedastic models. The residual variance for male calves was significantly greater than that for female calves and significant residual heteroskedasticity existed across herds, whether for linear model analyses of birth weights or for threshold model analysis of calving ease scores. However, the high correlation between posterior mean of sire effects from heteroskedastic and homoskedastic models indicated that there was no significant rerankings of sire genetic merit between the two models.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Robert Tempelman for his guidance, encouragement, permanent support and patience during these past five wonderful years as a doctoral student. Appreciation is also extended to Drs. Dennis Banks, Catherine Ernst, Joseph Gardiner and Frank Lupi for their encouragement and for serving on the guidance committee. Also I would like to express my sincere thanks to Department of Animal Science for kindly offering me an assistantship during my PhD program. I wish to thank Dr. Guilherme Rosa for his kindly help and advice during preparation of my dissertation. I greatly appreciate the logistical assistance provided by Dr. Peter Saama in Animal Breeding and Genetics Group Quantitative Genetics Lab. I also would like to thank my fellow graduate students Fernando Cardoso, David Edwards, Hugo Roman in Animal Science; Cengiz Caner in Food Packaging; Savas Berber in Physics and Astronomy and Dr. Jose Sanchez, Jeff Smeenk and Dr. Mohammed Khan in Crop and Soil Science for their friendship, encouragement and always being there to help me. I wish to thank Ersel and Sule Catal for friendship and support. I am thankful to Dr. Richard Harwood and the C.S. Mott Foundation for the financial support in the last term of my program. I also would like to thank Collage of Agriculture and Natural Resources (CANR) for their support through the Dissertation Completion Fellowship. I am thankful to Adnan Menderes University in Aydin, Turkey for their understanding and help. Finally I would like to thank my wife, Aysegul, my daughter, Mervenur and my son, Ismail Can, for their incomparable support and understanding.

PREFACE

Chapter 1 and Chapter 2 in this dissertation were written in the style required for publication in the *Journal of Animal Breeding and Genetics*. Chapter 3 and Chapter 4 were written in the style required for publication in the *Genetics Selection Evolution*.

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INTRODUCTION

Profitable cattle production requires careful cost control. A herd's cost of production is strongly associated with its general level of fitness and fertility (Banos 1999). Consequently, over the last two decades seedstock selection emphasis has been increasingly directed towards fitness traits such as conformation scores, calving ease, and stillbirth incidences.

Calving ease, or conversely calving difficulty, is particularly important for beef and dairy cattle production since calving problems, compared to successful unassisted calvings, generate additional costs well beyond parturition. Costs are immediately incurred, of course, as veterinary fees, increased labor costs, and potential loss of calf, but long term losses also accrue due to subsequent declines in dam health and fertility, directly resulting in reduced long-term productivity (Albera et al. 1999). Although all breeds experience calving difficulty to various degrees, incidence rates are particularly high in the heavy muscled Italian Piemontese breed (Carnier et al. 2000) relative to reported estimates on the continental and British breeds (Varona et al. 1999; Bennett and Gregory 2001). In the Germplasm Evaluation Program at the Roman L. Hruska U.S. Meat Animal Research Center (MARC) in Clay Center, NE (Wheeler et al. 1996) the Piemontese breed has been concluded to be the only breed out of 10 studied to "provide the greatest opportunity to produce, lean tender meat". Hence the importance of controlling calving difficulty in this breed cannot be understated. One strategy for improving calving ease is through genetic selection.

Genetic evaluation systems for normally distributed production characters have been based on well-characterized linear mixed models (Henderson 1973). Breeding sires are typically ranked by best linear unbiased predictions (BLUP) or, equivalently, empirical Bayes estimates of their corresponding random effects. Furthermore, variance component and derivative heritabilities are typically estimated using restricted maximum likelihood (REML), which has desirable properties relative to other methods (Mc Culloch and Searle 2001). Calving ease, however, is generally recorded as a 4 or 5 level ordinal category trait, such that normality assumptions are clearly violated. Abdel-Azim and Berger (1998) and Luo et al. (2001) have demonstrated that REML estimates of variance components based on linear mixed model analysis of categorical data yield biased estimates of heritabilities and genetic correlations.

A suitable model for genetic analysis of categorical data is the cumulative probit or threshold model adapted by Gianola and Foulley (1983) and Harville and Mee (1984). However, the proposed inference procedures rely upon rather strong asymptotic or approximate assumptions. Variance component estimation has been historically based on a joint maximization of the marginal posterior density of the variance components using an approximate invocation of the expectation-maximization (EM) algorithm (Harville and Mee 1984; Stiratelli et al. 1984). However, in various simulation tests of this method, some significant biases in heritability estimates were found (Hoeschele et al. 1987, Simianer and Schaeffer 1989). Furthermore, under the threshold model, breeding sire merit is typically estimated using elements of the joint posterior modes of these random effects, conditionally on estimated variance components. These joint posterior modes are intended to approximate the posterior means, shown to be optimal selection criteria by Fernando and Gianola (1986). Whether or not those approximations work well as intended for breed genetic evaluations is not clearly known.

Markov Chain Monte Carlo (MCMC) methods have facilitated exact sample Bayesian inference for many applications in animal breeding, including inference on categorical traits. In MCMC, inference on parameters is based on random but correlated draws from posterior distributions. Earlier studies have highlighted MCMC analysis for genetic parameter estimation in production traits (Wang et al. 1994a,b; Luo et al. 1999; Varona et al. 1999). The superiority of MCMC inference over, for example, approximate EM-based inference on variance components for categorical data under conventional threshold models has been demonstrated in simulation studies (Hoeschele and Tier 1995). MCMC allows additional modeling possibilities for quantitative genetic analyses of calving ease that have not yet been fully studied and exploited.

For example, it has been noted that preferential treatment may be partly responsible for the records of some high producing animals. Stranden and Gianola (1999) developed hierarchical Bayesian models based on a Student *t* distributed error structure to provide outlier-robustness on genetic evaluations. Calving ease is often subjectively scored by herdspersons on an ordinal scale such that data quality might conceptually be a greater issue here than for continuously distributed production characters. Albert and Chib (1993) proposed a cumulative *t* link model providing greater modeling flexibility relative to cumulative probit model for the analysis of ordinal categorical data. In animal breeding applications, a cumulative *t* link model might be considered to be an outlier-robust model to minimize the impact of outlying records on genetic merit predictions for calving ease on breeding sires.

As another example, many studies have indicated that residual variances are heterogeneous for normally distributed production characters across herds, sexes, and other factors (Hill et al. 1983; Ibanez et al. 1999). If this phenomenon is not properly taken into account (i.e. a homoskedastic error distribution is assumed), differences in within-subclass variances result in biased breeding value predictions such that a disproportionate numbers of animals may be selected from environments characterized by high variability. This bias has the potential effect of substantially reducing genetic progress due to breedstock selection based on these predictions (Hill 1984; Weigel and Gianola 1992).

A structural model for heterogeneity of residual variance on a conceptual underlying scale has been developed for the threshold model by Foulley and Gianola (1996). However, this model, as well as a subsequent model by Jaffrezic et al. (1999), invokes analytical approximations, which appear tenuous, particularly for the analysis of categorical data. Exact MCMC inference on residual heteroskedasticity is conceptually possible but requires development and testing.

Cumulative *t*-link and heterogeneous variance models need to be tested as alternatives to conventional threshold models used currently by the beef cattle industry for genetic evaluation of breeding sires for calving ease of their daughters as dams and progeny as calves. A hierarchical Bayesian framework seems to be suitable for the construction of these models, using MCMC for statistical inference.

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CHAPTER 1

Literature Review

INTRODUCTION

Dystocia, or calving difficulty, is defined as an abnormal or difficult birth requiring assistance (Manfredi et al. 1991). The percentages of dams requiring some assistance at calving range from 28.9% in American Gelbvieh (Varona et al. 1999) to 88.4% in Italian Piemontese cattle (Carnier et al. 2000), although these numbers may be further indicative of management differences as well. The percentages of dams requiring Caesarean section at calving range from are 0.4% in Holstein Fresian (Meijering 1984), to 13.7% in Italian Piemontese cattle (Carnier et al. 2000). Calving difficulty, or conversely calving ease, is scored subjectively according to its departure from a normal calving, the latter of which results with a healthy dam and a healthy calf without any human intervention (Meijering 1984). These scores are generally defined on an ordinal scale from 1 (unassisted calving) to 4 or 5 (Caesarean section), the score thereby reflecting the amount of required assistance at birth.

Injuries or suffocation resulting from difficult or delayed calving cause the death of many calves either at birth or immediately thereafter in spite of the fact that about 80% of all calves lost at birth are anatomically normal (Whitter and Thome 1995). In various beef breeds, calf mortality at or near the time of birth has been shown to be four times greater ($P<0.01$) in calves experiencing dystocia (20.4%) than in those not experiencing dystocia (5.0%) (Laster and Gregory 1973). In addition to the loss of the calf or dam, calving difficulties negatively impact cattle production through increased veterinary labor costs, subsequent dam health and fertility problems (i.e., increases in the postpartum interval or decreases in overall conception rate) and subsequently decreased dam milk production (Walker et al. 1994; Albera et al. 1999).

Anderson (1998) estimated that calving difficulty results in annual losses of 25 million dollars in the state of Nebraska and overall annual losses in the United States are estimated at between 500 million and 750 million dollars (Walker et al. 1994). Albera et al. (1999) itemized economic losses derived from market prices or supplied by veterinarians and Piemontese extension specialists in the computation of dystocia costs in Italian Piemontese cattle. These losses are highlighted in Table I. Since calving difficulty has both major direct and indirect costs on production, cattle breeders have an interest in genetic analysis of calving difficulty to selectively improve populations for better calving ease.

Genetic and environmental factors contribute to the cause and severity of calving difficulty. Figure 1 taken from Burfening (1991) flowcharts the complexity of this trait and serves to point out the numerous interacting factors that affect calving difficulty. As seen from Figure 1, calving ease is both a characteristic of the cow and of the calf. Furthermore, a breeding bull may influence calving ease either as a sire or as a maternal grandsire. For example, a calf's sire contributes to the calving ease as a characteristic of the calf through the sire's direct genetic effect. This particular genetic effect may be influenced by the birth weight, gestation length and shape of the calf as inherited from its sire. Sire breed differences for calving ease are known to exist. Laster et al. (1973) have shown in a study involving Hereford and Angus cows that calves sired by Charolais, Simmental, Limousin and South Devon bulls experienced significantly more calving difficulty than calves sired by Hereford, Angus and Jersey bulls ($P<0.01$). A maternal genetic effect, on the other hand, is determined by genes passed on by the sire to his daughter that affect her pelvic measures, uterine environment, hormonal control and other factors that determine her ability to calve easily as a dam. That same sire also passes on genes to his daughter's calf that directly influences its ability to be calved out easily (i.e. direct genetic effects).

Pollak and Freeman (1976) and Berger and Freeman (1978) determined that calf sex was an important source of variability for calving difficulty in Holsteins. This is not too surprising since bull calves are generally larger than heifer calves at birth. Laster and Gregory (1973) determined calf losses in various beef breeds to be higher in male calves (22.4%) than in female calves (16.3%) delivered from dams experiencing difficult births. However, they found no difference in calf mortality between sexes when calving was unassisted.

Calf birth weight is an important factor affecting calving difficulty. Laster et al. (1973) determined that the regression of calving difficulty on birth weight was highly significant ($P<0.005$). Birth weight is also genetically correlated to calving difficulty (Varona et al. 1999), which indicates that genetic selection against calving difficulty reduces birth weight. The effect of birth weight on calving difficulty is significant in heifers but as dams become older, the effect of birth weight becomes less important (Herring 1996). Calving difficulty in two-year-old dams (54% Hereford and Angus cows in U.S. Meat Animal Research Center, MARC and 30% Hereford cows in Colorado State University, CSU) is three to four times more frequent than in three-years-olds (16% in MARC and 11% in CSU), since the younger dams have not yet attained full physical or skeletal maturity (Meijering 1984). Calving difficulty problems are minimal when a dam reaches four to five years old. In an analysis of calving difficulty data collected over 14 years, Berger (1994) determined that fewer in Holstein cows needed assistance for calving in second (18.42%), third (16.97%) and later parities than in first parity (40.40%).

Season of calving also impacts calving difficulty. Berger (1994) reported that calving difficulty in Holsteins is more frequent during winter than in summer. Philipsson (1976) explained this by noting that summer is grazing season which enables cows to exercise on the pasture. In contrast, cows are confined and receive less exercise during the winter.

Pelvic opening of the dams also represents an important source of variation in the frequency of calving difficulties. Disproportion in size between the fetus and dam appears to be the major cause of dystocia. Thus, there is a critical need for adequate growth in heifers to allow an increase in pelvic area.

Both direct and maternal genetic variability appears to exist for calving ease based on studies reported in Table II. This table reports heritability and genetic correlation estimates by study, model and method of variance component estimation. These models and methods are discussed in more detail later. Although reported heritability estimates are highly variable, direct heritability estimates generally concentrate around intermediate values (0.15-0.20) with maternal heritability estimates being generally lower. The estimated genetic correlations between direct and maternal effects are also generally negative, thereby indicating that the ability of a female calf to be easily delivered from her own dam is antagonistic with that same female's ability to subsequently calve easily herself. Since calving ease and body dimensions are inherently related, a calf may be small at birth allowing her own easy delivery but then being small as a dam would have subsequent calving problems.

STATISTICAL MODELS FOR GENETIC EVALUATION OF CALVING EASE

A primary goal of breeding programs is to maximize genetic gain in animal traits affecting livestock production. Since the greatest selection differential is on sires in most beef cattle populations, particularly where the use of artificial insemination is prominent, accurate sire ranking is important. Achieving accurate sire selection requires inference on genetic parameters such as, for example, heritability, or the proportion of total variability that is genetic, whether for direct or maternal genetic effects. The greater the heritability, the greater the potential for genetic improvement of the character through selective breeding. For continuous production characters like weight gain, estimation of genetic parameters is typically carried out using restricted maximum likelihood (REML) under linear mixed models. In linear mixed models, the influence of fixed effects such as age, breed or sex along with genetic and other random effects are jointly inferred upon for the analysis of normally distributed traits. Predicted breeding values of individual animals using best linear unbiased prediction (BLUP) are useful for seedstock selection in livestock improvement programs (Henderson, 1973).

In addition to obvious production characters affecting farm revenue, economic efficiency in animal production can also be enhanced by considering genetic selection for health and reproductive fitness traits such as conformation score, calving ease and ovulation rate (Dematawewa and Berger, 1997). However, unlike production traits, fitness traits such as calving ease are often not continuous in their expression but are discrete. Thus, key multivariate normal distributional assumptions invoked under a linear mixed model analysis are violated, particularly when the number of ordinal categories is small; i.e. ≤ 5. Gianola (1982) argued against using BLUP to predict breeding values for ordinal data since estimated breeding values and residuals can be shown to be dependent upon each other. Furthermore, several recent studies illustrate that variance component estimation based on linear mixed models consistently yielded biased estimates of heritabilities and correlation coefficients in the analysis of categorical data (Abdel-Azim and Berger 1998; Luo et al. 2001).

Threshold models, more commonly known as cumulative link models in the statistics literature, are appropriate for the multifactorial analysis of ordinal categorical traits. Threshold models are probably best understood by the concept that the ordinal trait is influenced by an underlying liability or latent variable binned by various thresholds that impose a discontinuity on the visible expression of the trait (Falconer and MacKay, 1996). In Figure 2, for example, a liability value between the first and second thresholds maps to an observed category of assisted easy calving. The concept of the threshold model dates back to Wright (1934) who inferred upon the variability of the number of toe digits between and within strains of guinea pigs and hypothesized an underlying normal distribution of liability variables with strain-specific means and common variance. Using calving ease data as the application, both Gianola and Foulley (1983) and Harville and Mee (1984) proposed breeding value estimation procedures under a threshold mixed effects model based on the generalized linear model formalized by Nelder and Wedderburn (1972). Unlike the linear mixed model, the threshold mixed model does appropriately account for the multinomial distribution of calving ease data, conditional upon a "linked" function of both fixed and random effects as defined previously. The typical link function used for threshold mixed models in animal breeding is the cumulative probit function. The probit function is simply the inverse function of the standard normal cumulative density function (cdf). In a cumulative probit threshold model for the analysis of data with C ordinal categories, the cumulative probability, $\text{Prob}\left(J \le j\right)$, up to a certain ordinal score j, $1 \leq j \leq C$, on a subject is written as standard normal cdf of a linear function of the $(j-1)^{\text{th}}$ threshold parameter and the fixed and random effects associated with that subject. Using Figure 2, for example, the probability of a dam experiencing an easy unassisted calving or easier calving is modeled as the cdf of the first threshold plus any fixed or random effects that influence the magnitude of the liability variable. Gianola and Foulley (1983) developed scoring equations for the threshold mixed model under the Bayesian paradigm. These equations maximize the joint posterior density of the fixed and random effects, conditional upon known or estimated variance components. The corresponding joint modes are then reported as point estimates with standard errors based on the information matrix of this joint posterior density. These joint modal or maximum a posteriori (MAP) estimates are currently used for genetic evaluations on calving ease (Berger 1994; Wang et al. 1997).

Genetic evaluation models are of two broad types. The first model is the sire or sire and maternal grandsire model where calf records on, say, calving ease are connected directly to sires with genetic relationships identified only through known paternal ancestry. The second is the animal model where each record is connected directly to each calf identification with all known genetic relationships explicitly modeled. Whereas animal models are now predominantly used for genetic evaluation of production traits under a linear mixed model, sire or sire and maternal grandsire models are most often used for threshold mixed model analysis of calving ease data. If the predominant genetic relationship is that due to paternal halfsibs, there should be intuitively very little difference in sire genetic evaluations between those computed under a sire versus an animal model. Indeed, these models can be shown to be equivalent under a linear mixed model framework if the only genetic relationships are paternal half sibs on calves making the records. However, threshold animal models have been shown to lead to MAP estimates of breeding values that are much more biased than those determined under threshold sire models (Mayer, 1995), since the approximation invoked for MAP breaks down substantially when the number of records per individual in a model is small. Such a number on average is smaller in animal models than in sire models since there are generally many more unique calf identifications than unique sire identifications in a set of data.

BAYESIAN INFERENCE

Likelihood-based methods have been generally used to infer upon genetic parameters in animal breeding and genetics. However, recent theoretical and computational developments in Bayesian inference, such as Markov Chain Monte Carlo methods, have inspired researchers to increasingly use Bayesian methods in animal breeding and genetic applications.

In Bayesian inference, as with likelihood inference, the joint density of the data $\mathbf{y}$ is characterized by a probability distribution $p(\mathbf{y}|\boldsymbol{\theta})$. The quantity $\boldsymbol{\theta}$ denotes the vector of unknown parameters, including those that an investigator may wish to infer upon. A Bayesian model essentially consists of two parts. The first is the sampling distribution or likelihood function $p(\mathbf{y}|\boldsymbol{\theta})$ which is the information provided by $\mathbf{y}$ on $\boldsymbol{\theta}$. The second part is a prior distribution $p(\boldsymbol{\theta})$. In the Bayesian approach, researchers may have some prior knowledge about $\boldsymbol{\theta}$ which could be incorporated in the analysis using their specification of $p(\boldsymbol{\theta})$. This feature creates one main distinction between Bayesian and frequentist or likelihood approaches.

After combining the prior information $p(\boldsymbol{\theta})$ with the available information from data $p(\mathbf{y}|\boldsymbol{\theta})$, inference on $\boldsymbol{\theta}$ is based on the posterior distribution:

$$p(\boldsymbol{\theta}|\mathbf{y})=\frac{p(\mathbf{y}|\boldsymbol{\theta})p(\boldsymbol{\theta})}{p(\mathbf{y})}, \text{ where } p(\mathbf{y})=\int p(\mathbf{y}|\boldsymbol{\theta})p(\boldsymbol{\theta})d\boldsymbol{\theta}.$$

In the posterior distribution, p(y) is constant relative to inference on $\boldsymbol{\theta}$. Thus the posterior distribution can be written in the more compact form

$$p(\boldsymbol{\theta}|\mathbf{y}) \propto p(\mathbf{y}|\boldsymbol{\theta})p(\boldsymbol{\theta})$$

where $\propto$ denotes 'proportional to'. Herein lies another basic distinction between likelihood and Bayesian inference. Bayesian inference is conditional upon a single realization of **y** whereas likelihood or frequentist inference in based on conceptual repeated realizations of **y**. Furthermore, provided that $p(\theta|\mathbf{y})$ can be determined, Bayesian inference is exact for small samples whereas likelihood inference generally is not.

With $\boldsymbol{\theta}=(\theta_1,\theta_2,...,\theta_n)'$, marginal and conditional densities of any parameter θ_i can be obtained from the joint density $p(\theta_1,\theta_2,...,\theta_n)$. That is the marginal posterior density of any one parameter of interest, say θ_i, can be determined by:

$$p(\theta_i|\mathbf{y})=\int p(\theta_1,\theta_2,....,\theta_n|\mathbf{y})d\boldsymbol{\theta}_{-i}, \text{ where } \boldsymbol{\theta}_{-i}=(\theta_1,\theta_2,...,\theta_{i-1},\theta_{i+1},...,\theta_n)'.$$

When the posterior distribution is determined, inference on parameters can be made using any features of this distribution including location (mean, mode and median) and dispersion (variance and standard deviation).

VARIANCE COMPONENT ESTIMATION

Variance components and their derivative genetic parameters (i.e., direct and maternal genetic heritabilities and genetic correlation) in a threshold mixed model have been historically estimated using approximate marginal maximum likelihood (MML) techniques. The techniques are used to maximize the approximate marginal posterior density of the variance components. One historically popular technique in animal breeding is based upon an approximate invocation of the expectation-maximization (EM) algorithm proposed by Harville and Mee (1984), and Stiratelli et al. (1984). In simulation studies based on this algorithm, some biases were determined in heritability estimates. Hoeschele et al. (1987) reported that mean square error of MML was larger than that of REML when contemporary subclass sizes were small. Simianer and Schaeffer (1989) also determined EM-MML heritability estimates to be biased upwards by 50% in a binary trait simulation study when the mean subclass sizes were approximately 2.3 and 1.1 for each dataset. Hoeschele et al. (1987) and Simianer and Schaeffer (1989) considered that the approximation $\mathrm{u}|\mathrm{Y},\sigma_{\mathrm{u}}^2 \sim \mathrm{N}(\hat{\mathrm{u}},\mathrm{C}_{\mathrm{uu}})$, where u is breeding values, Y is ordinal categorical data, σ_{u}^2 is genetic variance, $\hat{\mathrm{u}}$ is the posterior mode estimates of breeding values and C_{uu} is the u-part of the inverse of the coefficient matrix, used in EM-MML is related to the bias of MML since this approximation is based on a normality assumption, which may not hold with small subclass sizes.

A second approximate MML algorithm is based on Laplace's method (Leonard 1982) and was first adapted to animal breeding by Tempelman and Gianola (1993). In a sire model simulation study by Tempelman (1998), binary data was generated from each of three populations (additive genetic variance = 0.20, 0.60 or 1.00). Laplacian MML estimates were determined to be much less biased than EM-MML estimates of variance components along with 20 to 30% less relative error. Since the Laplacian procedure is analogous to the derivative-free REML procedure introduced by Graser et al. (1987), it facilitates hypothesis testing of variance components via marginal likelihood ratio tests (Tempelman, 1998).

Markov Chain Monte Carlo (MCMC) is a general method for the simulation of random variables from probability density functions known only up to proportionality (Geyer 1992) and thus is particularly well suited to Bayesian inference. The root of MCMC methods can be traced back to the application of Metropolis et al. (1953) in physics. The Gibbs sampler introduced by Geman and Geman (1984) is simply one implementation of MCMC whereby the joint posterior distribution of all unknowns can be derived from knowledge of the distributions of each unknown parameter conditional on all other parameters and the data. These distributions are typically referred to as fully conditional posterior distributions (FCD's). Due to the Markov Chain properties, MCMC samples are autocorrelated such that the information content of these samples is less than if the samples could be drawn independently. This problem can be readily overcome, however, by simply drawing more MCMC samples. In contrast to the approximate EM-MML algorithm, which simply yields point estimates, MCMC methods can retrieve the entire posterior distribution of any unknown parameter of interest (Sorensen et al. 1994).

Wang et al. (1993, 1994a) first used the Gibbs sampler in animal breeding, applying the method to both linear mixed sire and animal models. Sorensen et al. (1994) and Wang et al. (1994b) implemented Gibbs sampling in a method for drawing Bayesian inferences about selection response in livestock populations over time. Jensen et al. (1994) extended the use of the Gibbs sampler to models that involve covariance components, such as that would exist between direct and maternal additive genetic effects for beef production traits.

The Gibbs sampler was introduced for the analysis of binary data by Zeger and Karim (1991). Extensions of their procedure for the analysis of ordinal categorical responses were presented by Albert and Chib (1993), who used it in conjunction with data augmentation (Tanner and Wong 1987; Gelfand et al. 1992) in a somewhat computationally simpler strategy relative to Zeger and Karim (1991). Sorensen et al. (1995) subsequently adapted Albert and Chib's work to quantitative genetic inference on ordinal data. By augmenting the observed categorical data with the MCMC generated underlying liability variables, the FCD's for all fixed and random effects and variance components were found to have the same simple forms as in the linear mixed model, using liability variables generated from their FCD as, essentially, the data (Sorensen et al. 1994). Van Tassell et al. (1998) further extended the Gibbs sampler for multiple trait analysis of several continuous and ordered categorical traits, applying their sampler to the joint analysis of twinning and ovulation rates from a herd of cattle selected for twinning rate at the U.S. Meat Animal Research Center.

Hoeschele and Tier (1995) demonstrated that MCMC point estimates (posterior means) of variance components have frequency properties that are superior to approximate EM-MML estimates in simulated ordinal categorical data characterized by small contemporary subclass sizes (i.e. small herds). However, these differences were shown to be increasingly smaller with larger sample sizes.

Varona et al. (1999) analyzed calving difficulty scores from Gelbvieh cattle by using a threshold animal model using MCMC to obtain the marginal posterior mean and standard deviation of the direct and maternal heritabilities and the direct-maternal genetic correlation. The posterior means ± standard deviations of the direct and maternal heritabilities for calving difficulty were 0.23±0.036 and 0.10±0.018, respectively. The posterior mean of genetic correlation (–0.36±0.090) demonstrated an antagonistic genetic relationship between the direct and maternal effects for calving ease. Luo et al. (2001) also studied statistical models including direct and maternal genetic effects for calving ease scores using Gibbs sampling for inference. Inference properties on heritabilities and genetic correlations comparing animal models versus sire and maternal grandsire models and threshold mixed models versus linear mixed models were compared. They concluded that linear mixed models produced significant downward or upward biased ($P<0.05$) point estimates of heritabilities in contrast to point estimates derived using threshold mixed models. Also, threshold sire and maternal grandsire models yielded smaller mean squared error of heritability estimates than a threshold animal model. Furthermore, treating herd-year-season (HYS) as random effects in the threshold sire models reduced the variance of estimates of genetic parameters for the categorical traits. Luo et al. (2001) concluded that the threshold sire and maternal grandsire model was most appropriate for the quantitative genetic analysis of calving ease.

ROBUST MIXED LINEAR MODELS

For normally distributed data or alternatively for underlying liability variables in threshold mixed models, residual terms are typically assumed to be normally distributed with zero mean and common variance in animal breeding applications. This assumption, however, may make the resulting analysis vulnerable to the presence of outliers (Rogers and Tukey 1972, Lange et al. 1989). Heavier-tailed densities (such as the univariate or multivariate Student *t* distributions) are viable alternatives to the Gaussian one. The *t* family of distributions [$t(\mu,\sigma^2,\nu)$] is characterized by three parameters: center μ, scale σ^2 and degrees of freedom parameter $\nu \in (0,\infty)$ that determines the heaviness of the tails (Gelman 1995). When $\nu = 1$, the *t* distribution is the Cauchy distribution with a very thick tail, infinite mean and infinite variance. Conversely, when $\nu \to \infty$, the *t* distribution approaches the lighter-tailed normal distribution. Having a thicker tail, the *t* distribution can provide robustness against unusual or outlying observations when used to model the density of the residual terms.

Lange et al. (1989) considered the *t*-distribution as a useful extension of the normal distribution for statistical modeling of datasets having outliers. A maximum likelihood approach was used for parameter estimation including the degrees of freedom parameter. Numerous datasets were analyzed based on the maximum likelihood strategy for a general *t*-distributed error model. Generally, the *t* model was found to fit much better than a normal model based on the likelihood ratio test. The asymptotic standard errors for the location parameter estimates under the *t* model also were generally smaller compared to the normal models. Reasonable estimates of degrees of freedom were obtained for all datasets, except for a radioimmunoassay dataset. In a nonlinear regression analysis of radioimmunoassay dataset, the maximum likelihood estimate of the degrees of freedom parameter was 0.29, which was concluded to be not very satisfactory. Lange et al. (1989) concluded that the low estimate stemmed from attempting to accommodate one very extreme outlier. When that outlier was removed, the resulting estimate increased to 1.2. Fraser (1979) suggested that maximum likelihood estimation of degrees of freedom is not advisable when degrees of freedom estimation goes much below 1 suggesting that the *t*-model is not well suited to data with extreme outliers. Fraser (1979) further suggested that in problems with small sample sizes, researchers might fix the degrees of freedom at some predetermined value, such as 4, rather than attempt to estimate the degrees of freedom simultaneously with other parameters. Based on the results from different analysis, they concluded that outliers and robustness can be handled by the maximum likelihood estimator for all the parameters in the *t*-distributed error model using the EM algorithm.

Lange and Sinsheimer (1993) extended the work by Lange et al. (1989) further by considering alternative heavy-tailed distributions to the Student *t*. Each of the models considered in their paper, including the logistic, slash, *t* and contaminated normal distributions, were shown to be derived as scale mixtures of normals. More specifically, given that the residual terms e_i are specified conditionally as $e_i \sim N\left(0, \frac{\sigma_e^2}{\lambda_i}\right)$, $i=1,2,\ldots,n$, alternative heavy-tailed residual densities can be marginally specified by alternative distributions on λ_i. For example, a Student *t* distribution is represented as a scale mixture of normals with Gamma distributed scaling factors $\lambda_i \sim Gamma\left(\frac{\nu}{2}, \frac{\nu}{2}\right)$, ν being the degrees of freedom (Lange et al. 1989). Alternatively, the slash distribution is characterized by scaling factors having the density $p(\lambda_i \mid \nu) = \nu\lambda_i^{\nu-1}$, , $i = 1,2,\ldots,n$. Under a contaminated normal error model, each residual is drawn from a mixture of two populations based on $\text{Prob}(\lambda_i = \lambda \mid \phi, \gamma) = \gamma$ if $\lambda = \phi$ or $1-\gamma$, if $\lambda = 1$. In a logistic error model, the probability is transformed to odds to remove the upper bound and then taking the logarithm of odds also removes the lower bound for the linear function of the explanatory variables. Lange and Sinsheimer (1993) chose the following logistic model $\mu_i = \theta_1 / \left(1 + e^{\theta_2 + \theta_3 \ln(x_i) + \theta_4 [\ln(x_i)]^2}\right)$ for their analysis. Using maximum likelihood in large datasets, the authors found that the *t*, slash and contaminated methods showed great promise in muting the effects of outliers. The slash and *t*-models had particularly superior estimation properties while the contaminated and logistic model were less satisfactory. However, in the analysis of radioimmunoassay data, Lange et al. (1989) found potential problems with the *t* and slash error models and suggested that the best alternative with a data set of this nature may be to discard the outliers and simply use the normal error models.

Geweke (1993) considered methods for Bayesian inference in econometric models in which errors were independent and identically *t*-distributed using the Gibbs sampler. Posterior odds ratios were calculated for *t*-error models having different degrees of freedom versus a normal error model. Geweke applied these models to fourteen macroeconomic time series datasets and found that the posterior odds ratio always heavily favored the independent Student-*t* error model over the normal error model.

In animal breeding and genetics, it has been noted that preferential treatment commonly influences the records of high producing or economically valuable animals and consequently, their predicted breeding values (Stranden 1996). Stranden and Gianola

(1998) simulated the effect of preferential treatment of cows for milk production in four herds of a multiple ovulation and embryo transfer scheme under selection. Three mixed effect linear models were compared in terms of their ability to handle preferential treatment: the classical Gaussian model, a model with multivariate *t*-distributed error clustered by herd, and a model with independent *t*-distributed error. The posterior distributions of all parameters were obtained using the Gibbs sampler. The three models were found to have similar performance in the absence of preferential treatment. Conversely, when the preferential treatment was prevalent and substantial in effect, the univariate *t*-model lead to substantially less biased inference on breeding values and genetic trends than those obtained with the Gaussian model.

Stranden and Gianola (1999) also presented a Bayesian approach for inferences about parameters of mixed effects linear models with *t*-distributed error effects in quantitative genetic application. Data was generated based on a preferential treatment process. The univariate *t*-model for the errors led to better estimates of additive genetic and error variances than either a herd-clustered *t*-model or a Gaussian sampling process. Using a univariate *t*-model, posterior distributions of breeding values were found to be sharper and the posterior mean estimates of heritabilities were closer to the true values compared to estimates derived from the other two models.

Rosa (1999) considered the application of robust mixed linear models based on *t*-distribution, slash and contaminated normal error distributions to pup birth weight from reproduction toxicology study. Marginal posterior densities of degrees of freedom, for the *t* and slash error distributions, were determined to be concentrated about small values, suggesting the inadequacy of the Gaussian distribution. Rosa (1999) also computed Bayes factors to verify the better fit of the long-tailed distributions to this data set.

In statistical mapping of quantitative trait loci (QTL), a common assumption is normally distributed phenotypic observations; any deviation from this assumption can affect power and robustness of QTL detection. Von Rohr and Hoeschele (2002) demonstrated the application of a skewed Student-*t* sampling model under four different error distributions and determined that residual, additive QTL and dominance QTL variance estimates were much closer to the true value when the analysis was performed with the skewed Student-*t* model rather than with normal model. Replacement of the normal by a skewed Student-*t* penetrance function also clearly improved the accuracy of parameter estimation. Thus, their results indicated substantial benefits of heavy-tailed skewed error models for QTL mapping.

Albert and Chib (1993) considered a cumulative *t*-link function, rather than a cumulative probit link function for the analysis of ordinal categorical data. This specification is equivalent to specifying the underlying latent variables in a threshold model to be *t*-distributed rather than normally distributed. Gianola and Sorensen (1996) extended Albert and Chib's (1993) work to describe a hierarchical Bayes model with correlated random effects suitable for quantitative genetic analysis of categorical data. Albert and Chib (1993) also presented Gibbs sampling schemes for models where the latent distribution was either univariate or multivariate *t*, and also considered Bayes factors for contrasting different models as well as for identification of outliers.

HETEROSKEDASTIC MIXED EFFECTS MODELS

An important assumption in most genetic evaluation models is that variance components associated with random effects are constant across all environmental conditions. However, the existence of heterogeneous variance, or heteroskedasticity, for milk production (Hill et al. 1983; Ibanez et al. 1999), growth performance (Garrick et al. 1989), and conformation (Robert-Granie et al. 1997) has been firmly established. More recently, work on estimating heteroskedasticity on the underlying scale in threshold models have been investigated in animal breeding (Foulley and Gianola 1996; Jaffrezic et al. 1999; Ducrocq 2000).

A number of possible reasons for heteroskedasticity have been suggested, including a positive relationship between herd means and variance, spatial gradients in residual variability across geographical regions, and temporal gradients in residual variability within herds due to changes in herd management. If heteroskedasticy is not properly taken into account, differences in within-subclass variances can result in biased breeding value predictions and disproportionate numbers of animals selected from environments characterized by high variability, thereby reducing genetic progress (Hill 1984; Weigel and Gianola 1992).

Alternative methods have been proposed to take into account heterogeneity of variance in quantitative genetics and animal breeding. For continuous production data, a logarithmic transformation can be used to alleviate the heterogeneous variance problem if the variances are a simple function of the mean of trait. Scaling of observations by the estimated standard deviations was proposed by Hill (1984) as another method of accounting for heterogeneous variance.

Heterogeneity of genetic and residual variances can be accounted for in genetic evaluation using BLUP, provided that these variance components are known (Gianola 1986). However, variance components are rarely known and need to be estimated. Since most preferred methods of variance components estimation, including ML and REML, rely on asymptotic properties, such procedures may not yield reliable estimates if variance components are estimated separately for each of many small subclasses (Weigel and Gianola 1992). This was demonstrated by Winkelman and Schaeffer (1988) who used REML and ANOVA to estimate within-herd genetic and residual variances.

Gianola et al. (1992) presented a Bayesian approach to deal with heterogeneity of residual variances with respect to some criterion of classification (strata) of the data. In their model, variance components (or variance covariance matrices) were assumed to have prior inverted chi-square (or inverted Wishart) distribution. The resulting empirical Bayes estimates of within-herd residual variances can be essentially shown to be weighted averages of the residual variance using data from the herd (i.e. REML) and the average across-herd residual variance. Gianola et al. (1992) indicated that when the amount of information in a particular herd stratum is large, the REML part of the estimator dominates; otherwise, the average across herd estimate dominates.

Foulley et al. (1992) proposed a structural linear model for assessing the source of heterogeneity of residual variances in Gaussian mixed linear models. Their procedures are based on the concept of a log link function, $\gamma_i = \ln \sigma^2_{e_i} = \boldsymbol{m}_i'\boldsymbol{\lambda}$, for variance components where $\sigma^2_{e_i}$ is the residual variance in subclass i, and $\boldsymbol{m}_i$ is a known incidence matrix for the unknown vector $\boldsymbol{\lambda}$ of dispersion parameters. The marginal likelihood (marginal posterior density of $\boldsymbol{\lambda}$) is maximized with respect to $\boldsymbol{\lambda}$ to determine point estimates. Hypothesis testing of any of the dispersion parameters in λ are then based on a marginal likelihood ratio test against subset models. The estimation algorithms in Foulley et al. (1992) showed remarkable similarities to the mixed model equations of Henderson.

San Cristobal et al. (1993) extended the method of Foulley et al. (1992) by identifying potential multifactorial sources of heterogeneity of residual and genetic variances in mixed linear Gaussian models. They developed the model based on a structural linear model for log residual and genetic variances as a function of fixed and random effects, just as is done for location parameters in a regular linear mixed effects model.

Foulley and Gianola (1996) adopted the structural linear model and log link function for heterogeneity of residual variance of underyling liabilites in the cumulative probit threshold model. Approximate statistical inference and hypothesis testing on all dispersion parameters and goodness of fit was again based on a marginal likelihood test. Foulley and Gianola (1996) applied their method to calving ease scores from the US Simmental breed and concluded that the heteroskedastic threshold model had a better fit to the data than the standard threshold model.

Jaffrezic et al. (1999) also used a structural linear model on log-variance to infer upon heterogeneity of residual variances in mixed threshold model. For parameter estimation they presented an approximate quasi-score approach including two steps: i) a marginalization with respect to the random effects leading to quasi-score estimators, ii) an approximation of variance-covariance matrix of the observations.

Ducrocq (2000) analyzed the calving ease data of French dairy breeds (Normande and Montbeliarde) using the heteroskedastic threshold model as proposed by Foulley and Gianola (1996). He first selected a satisfactory model to describe the effects of environmental factors on the location and dispersion parameters of the underlying liability variables. Four random effects were then added: sire of calf, sire of dam, dam (within sire of dam) and herd-year-season, assuming homogeneous ratios of variance components across environments. Accounting for heterogeneity of the residual variance in the analysis significantly improved all model fit criteria (likelihood ratio, AIC and chi-square statistics). He determined that direct and maternal heritability estimates were similar for both breeds but were substantially lower than those obtained by Manfredi (1990). Direct heritabilities were 5.4% in both breeds, while maternal heritabilities were very low (around 3%).

The specific objectives for this dissertation were to

1) Compare variance component, genetic parameter and breeding value estimates based on the two marginal maximum likelihood procedures (EM and Laplace), and MCMC using a threshold sire-maternal grandsire model in order to assess the relative need for MCMC methods in a national genetic evaluation system for calving ease.
2) Assess the potential utility of outlier-robust threshold models in simulated and actual calving ease data.

3) Develop and apply a Bayesian structural multiplicative model on residual variances for observed and augmented variables in heteroskedastic generalized linear mixed models.

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Table I. Itemized dystocia costs (Albera et al. 1999).

Parameter	Dollars*
Cost of caesarean section	99.99
Labor of the farmer per hour	4.58
Price of a newborn male calf	545.46
Price of a newborn female calf	409.12
Cost of involuntary culling after first calving	306.40
Cost of involuntary culling after other calvings	483.67

*Based on 1Euro = $ 0.8802.

Table II. Direct heritability (h^2_d), maternal heritability (h^2_m), and direct-maternal genetic correlation (r_g) estimates ± standard errors, where available, for calving ease score.

Study	Model	Method	Breed	h^2_d	h^2_m	r_g
Meijering (1985)	Linear	MINQUE	Holstein	0.09	-	-
Manfredi et al. (1991)	Threshold	Tilde-hat	Normande	0.08	0.11	0.15
			Holstein	0.07	0.07	-0.10
Dong et al. (1991)	Threshold	-	Simmental	0.18	0.19	-0.16
McGuirk et al. (1998)	Linear	REML	Charolais	0.11±0.02	-	-
			Hereford	0.07±0.01	-	-
			Limousin	0.04±0.01	-	-
McGuirk et al. (1998)	Threshold	REML	Charolais	0.20±0.03	-	-
			Hereford	0.16±0.03	-	-
			Limousin	0.15±0.03	-	-
McGuirk et al. (1999)	Linear	REML	Holstein	0.05±0.00	-	-
McGuirk et al. (1999)	Threshold	REML	Holstein	0.12±0.01	-	-
Varona et al. (1999)	Linear	MCMC	Gelbvieh	0.19±0.03	0.07±0.02	-0.35±0.08
Varona et al. (1999)	Threshold	MCMC	Gelbvieh	0.23±0.04	0.10±0.02	-0.36±0.09
Luo et al. (1999)	Linear	MCMC	Holstein	0.05	0.04	-0.16
Carnier et al. (2000)	Linear	REML	Piemontese	0.19±0.01	0.09±0.01	-0.48±0.04
Ducrocq (2000)	Threshold	REML	Montbeliarde	0.05	0.03	-0.16
	Heterogeneous		Normande	0.05	0.03	-0.04
Bennett and Gregory (2001)	Linear	REML	Angus	0.29	0.14	-
			Braunvieh	0.61	0.07	-
			Charolais	0.26	0.25	-
			Gelbvieh	0.32	0.40	-
			Hereford	0.46	0.35	-
			Limousin	0.12	0.25	-
			Pinzgauer	0.72	0.05	-
			Red Poll	0.27	0.27	-
			Simmental	0.34	0.28	-

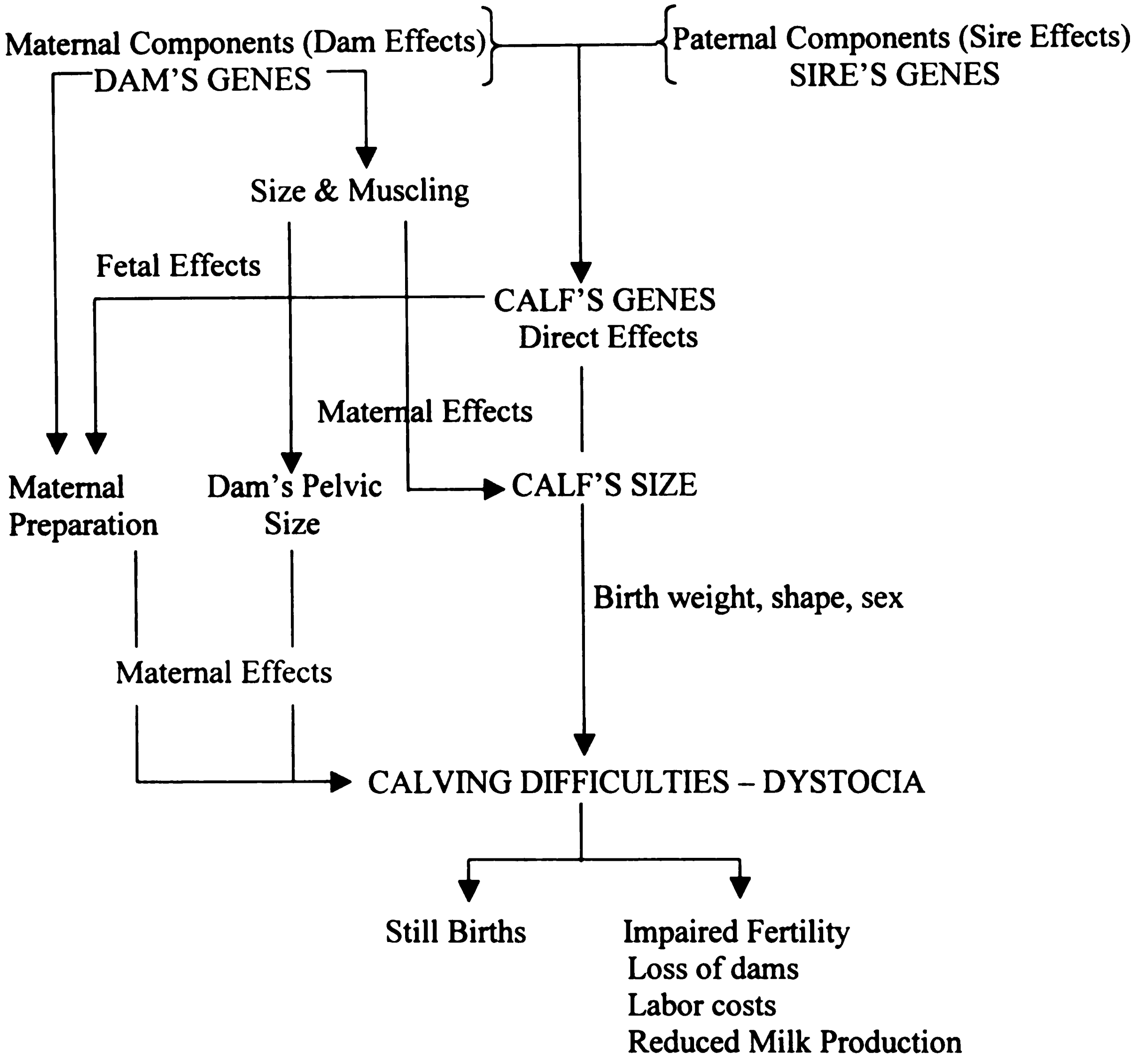

Figure 1. A flowchart interaction of direct additive and maternal genetic effects with other factors in terms of their effect on calving difficulty (Burfening 1991).

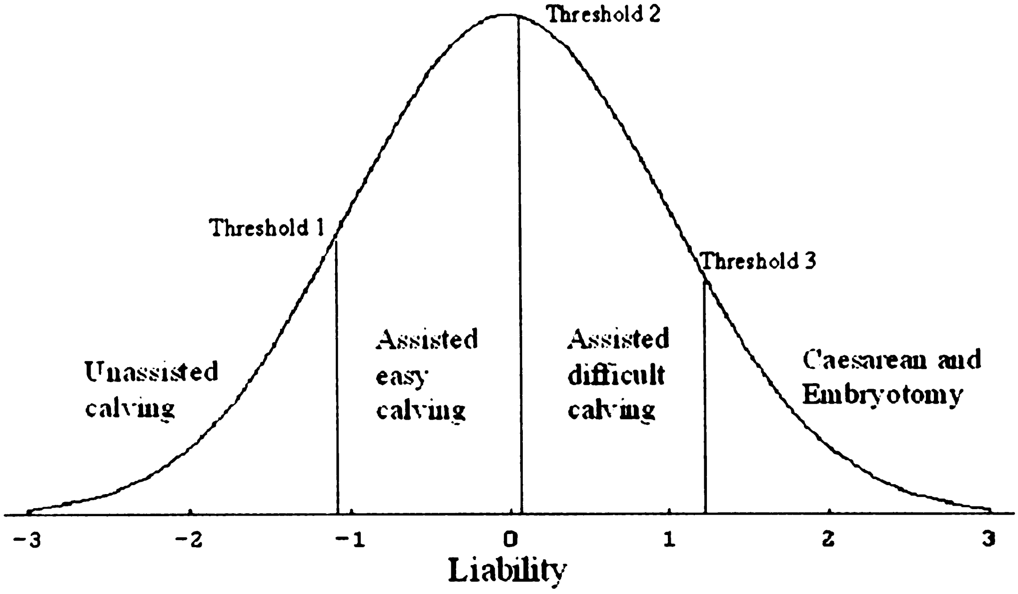

Figure 2. Mapping of underlying liabilities to observed calving ease phenotypes. Thresholds 1, 2, and 3 delimit normally distributed underlying liabilities into 4 calving ease phenotypes (unassisted calving, assisted easy calving, assisted difficult calving, and Caesarean and embryotomy).

CHAPTER 2

Bayesian Inference Strategies for the Prediction of Genetic Merit Using Threshold Models with an Application to Calving Ease Scores in Italian Piemontese Cattle

ABSTRACT

First parity calving difficulty scores from Italian Piemontese cattle were analyzed using a threshold mixed effects model. The model included the fixed effects of age of dam and sex of calf and their interaction and the random effects of sire, maternal grandsire, and herd-year-season. Covariances between sire and maternal grandsire effects were modeled using a numerator relationship matrix based on male ancestors. Field data consisted of 23,953 records collected between 1989 and 1998 from 4,741 herd-year-seasons. Variance and covariance components were estimated using two alternative approximate marginal maximum likelihood (MML) methods, one based on expectation-maximization (EM) and the other based on Laplacian integration. Inferences were compared to those based on three separate runs or sequences of Markov Chain Monte Carlo (MCMC) sampling in order to assess the validity of approximate MML estimates derived from data with similar size and design structure. Point estimates of direct heritability were 0.24, 0.25 and 0.26 for EM, Laplacian and MCMC (posterior mean), respectively whereas corresponding maternal heritability estimates were 0.10, 0.11 and 0.12, respectively. The covariance between additive direct and maternal effects was found to be not different from zero based on MCMC-derived confidence sets. The conventional joint modal estimates of sire effects and associated standard errors based on MML estimates of variance and covariance components differed little from the respective

posterior means and standard deviations derived from MCMC. Therefore, there may be little need to pursue computation-intensive MCMC methods for inference on genetic parameters and genetic merits using conventional threshold sire and maternal grandsire models for large datasets on calving ease.

INTRODUCTION

Calving ease has a significant economic impact on beef and dairy production through increased risk to the survival of both calf and cow (McGuirk et al. 1998). The Italian Piemontese breed has a particularly high percentage of difficult calvings (Carnier et al. 2000) relative to reported estimates from other breeds (Varona et al. 1999; Bennett and Gregory 2001). Accurate inference on genetic parameters and genetic merit are important precursors for effective sire selection strategies to improve calving ease.

The threshold mixed model developed by Gianola and Foulley (1983) is one example of generalized linear mixed models (Breslow and Clayton 1993) which have become increasingly popular for the multifactorial mixed effects analyses of non-normal phenotypes. There have been a number of recent studies illustrating advantages of threshold mixed models over linear mixed models for the analysis of ordinal calving ease data (Luo et al. 2001; Rameriz-Valverde et al. 2001).

Empirical Bayes or maximum a posteriori (MAP) estimates of breeding values are based upon a joint maximization of the posterior density of fixed and random effects conditioned upon variance components being known, or set equal to their estimates (Foulley et al. 1987). These MAP estimates are currently used for published genetic evaluations on calving ease (Berger 1994; Wang et al. 1997). Variance components and their derivative genetic parameters in a threshold mixed model have been historically estimated using approximate and deterministic marginal maximum likelihood (MML) techniques. One such technique is based upon an approximate invocation of the expectation-maximization (EM) algorithm as proposed by Harville and Mee (1984) and Stiratelli et al. (1984). Some significant biases on heritability estimates using this algorithm were reported in simulation studies conducted by Hoeschele et al. (1987), Hoeschele and Gianola (1989) and Simianer and Schaeffer (1989), particularly when contemporary subclass sizes were small and genetic parameters were large in magnitude.

A second approximate MML algorithm is based on Laplace's method and was first adapted to animal breeding by Tempelman and Gianola (1993). In a sire model simulation study, Tempelman (1998) determined that Laplacian MML estimates tended to be much less biased than EM-MML estimates of variance components. Since the Laplacian procedure is analogous to the derivative-free REML procedure introduced by Graser et al. (1987), it also facilitates hypothesis testing of variance components via marginal likelihood ratio tests (Tempelman, 1998).

Markov Chain Monte Carlo (MCMC) techniques allow small sample inference and have been utilized in animal breeding and genetics (Sorensen et al. 1995; Hoeschele and Tier 1995; Varona et al. 1999; Luo et al. 1999; Luo et al. 2001). The relative improvements in properties of MCMC point estimates (posterior means) of variance components relative to approximate MML estimates from data characterized by small contemporary subclass sizes have been demonstrated in simulation studies by Hoeschele and Tier (1995), although differences were shown to be increasingly smaller with larger sample sizes. Even so, in the largest simulated dataset considered by Hoeschele and Tier

(1995), herd-year-season (HYS) subclasses were large in average size (>50) and maternal effects were not considered. In contrast, many breed association datasets used for genetic evaluations are large yet characterized by many small contemporary subclass sizes. The computing requirements for MCMC are not trivial for large datasets, and the need for MCMC, not only for inference on variance components but as well as on breeding values, needs to be validated. Furthermore, execution of MCMC requires far greater care than conventional MAP implementations for national genetic evaluations.

The objectives of this study were 1) to determine and compare variance component and corresponding genetic parameter estimates for calving ease scores in an Italian Piemontese population using the two MML procedures (EM and Laplace), and MCMC based on a threshold sire-maternal grandsire model, and 2) to compare conventional MAP estimates of breeding values and approximate standard errors with corresponding MCMC posterior means and standard deviations in order to assess the relative need for MCMC methods in a national genetic evaluation system for calving ease, and 3) to demonstrate the utility of a Metropolis-Hastings update on improving MCMC mixing on the threshold parameters.

MATERIALS AND METHODS

Data

First parity calving ease scores recorded on Italian Piemontese cattle from January, 1989 to July, 1998 by ANABORAPI (Associazione Nazionale Allevatori Bovini di Razza Piemontese, Strada Trinità 32a, 12061 Carrù, Italy) were used in this study. Only herds with at least 50 records over that time period were considered, leaving a total of 23,953 records. Calving difficulty was coded into five categories by breeders and recorded by technicians who visited the farmers monthly: 1) unassisted delivery, 2) assisted easy calving 3) assisted difficult calving 4) caesarean section and 5) foetotomy. Categories 4 and 5 were combined for analyses as the incidence of foetotomy was less than 0.5%. The general frequencies of first parity calving ease scores in the data set were 2,747 (11.47%) for unassisted delivery, 14,131 (58.99%) for assisted easy calving, 3,683 (15.38%) for assisted difficult calving and 3,392 (14.16%) for caesarean section and foetotomy.

The effects of age of dam and sex of calf and their interaction were modeled by combining eight different age groups (20 to 23, 23 to 25, 25 to 27, 27 to 29, 29 to 31, 31 to 33, 33 to 35, and 35 to 38 months) with sex of calf for a total of 16 nominal subclasses. Herd-year-season (HYS) subclasses were created from combinations of herd, year, and two different seasons (from November to April and from May to October) as in Carnier et al. (2000), except that HYS was treated as random in this study.

The total number of identified sires in the pedigree file was 9,090. A total of 1,817 of these sires were identified as being both calf sires and calf maternal grandsires, thereby indicating the density of genetic relationships accruing from selection over time. After pedigree pruning (i.e. treating as unknown those sires that do not have daughters with calving ease records and appear in the pedigree file only once), the number of sires that uniquely contributed to inference on genetic parameters and breeding values was determined to be 3,624.

Threshold Model

Calving ease scores are determined by unobserved underlying continuous variables or liabilities and a set of fixed thresholds, $\tau_1 < \tau_2 .... < \tau_{m-1}$, with $\tau_0 = -\infty$ and $\tau_m = \infty$, where m is the number of categories. An observed calving ease score is dependent upon underlying variable, which is bounded between two unobserved thresholds (Gianola and Foulley 1983). More specifically, calving ease scores y_i for individual i, in this study are defined by the following bins for U_i, the underlying liability for individual i:

$$y_i = \begin{cases} 1 & \tau_o < U_i \leq \tau_1 \\ 2 & \tau_1 < U_i \leq \tau_2 \\ 3 & \tau_2 < U_i \leq \tau_3 \\ 4 & \tau_3 < U_i < \tau_4 \qquad i = 1....n \end{cases} \tag{1}$$

A linear model is used to characterize the distribution of the unobserved liabilities:

$$\mathbf{U} = \boldsymbol{\eta} + \mathbf{e} \tag{2}$$

where $\mathbf{U}$ is a n x 1 vector of liabilities on calving difficulty, $\boldsymbol{\eta} = \mathrm{E}(\mathbf{U})$ is the vector of mean liabilities, and $\mathbf{e}$ is a vector of liability residuals with $\mathbf{e} \mid \sigma_e^2 \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$.

In addition to the specifications on τ_0 and τ_4, identifiability constraints require that one of τ_1, τ_2, or τ_3 be set to an arbitrary constant; in this case, we set $\tau_1 = 0$ such that the vector of estimable thresholds is $\boldsymbol{\tau} = \begin{bmatrix} \tau_2 \\ \tau_3 \end{bmatrix}$. An additional identifiability constraint was satisfied by setting $\sigma_e^2 = 1$ (Gianola and Foulley 1983).

The mean liability is written as a linear combination of fixed and random factors as typical of a sire and maternal grandsire model,

$$\boldsymbol{\eta} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{s} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{h} \tag{3}$$

where $\boldsymbol{\beta}$ is a p x 1 vector of fixed intercept and age-sex effects, **s** is a q_a x 1 vector of random sire effects, **m** is a q_a x 1 vector of random maternal grandsire (MGS) effects, **h** is a q_h x 1 vector of random HYS effects, and **X**, $\mathbf{Z}_1$, $\mathbf{Z}_2$, and $\mathbf{Z}_3$ are known incidence matrices. We assume:

$$\begin{pmatrix} \mathbf{s} \\ \mathbf{m} \end{pmatrix} \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A}\right)$$

and

$$\mathbf{h} \sim N\left(\mathbf{0}, \mathbf{I}\sigma_h^2\right)$$

where $\mathbf{G}_0 = \begin{pmatrix} \sigma_s^2 & \sigma_{sm} \\ \sigma_{sm} & \sigma_m^2 \end{pmatrix}$, with σ_s^2 denoting the sire variance, σ_m^2 denoting the maternal grandsire variance, σ_{sm} denoting the sire-maternal grandsire covariance, and σ_h^2 denoting the HYS variance. Furthermore, $\otimes$ denotes the Kronecker product (Searle 1982), and **A** is the numerator additive relationship matrix between sires due to identified male ancestors (Henderson 1976). Also, **h** is assumed independent of **s** and **m.**

MML Using the EM Approach

Variance components were first estimated by MML using the EM-type algorithm of Harville and Mee (1984). Applied to the problem at hand, the EM algorithm is based on iterating through

$$\sigma_s^2 = \frac{\hat{\mathbf{s}}'\mathbf{A}^{-1}\hat{\mathbf{s}} + trace\left(\mathbf{A}^{-1}\tilde{\mathbf{C}}_{ss}\right)}{q_a} \tag{4a}$$

$$\sigma_m^2 = \frac{\hat{\mathbf{m}}'\mathbf{A}^{-1}\hat{\mathbf{m}} + trace\left(\mathbf{A}^{-1}\tilde{\mathbf{C}}_{mm}\right)}{q_a} \tag{4b}$$

$$\sigma_{sm} = \frac{\hat{\mathbf{s}}'\mathbf{A}^{-1}\hat{\mathbf{m}} + trace\left(\mathbf{A}^{-1}\tilde{\mathbf{C}}_{sm}\right)}{q_a} \tag{4c}$$

and

$$\sigma_h^2 = \frac{\hat{\mathbf{h}}'\hat{\mathbf{h}} + trace\left(\tilde{\mathbf{C}}_{hh}\right)}{q_h} \tag{4d}$$

Writing $\boldsymbol{\theta}' = \begin{bmatrix}\boldsymbol{\tau}' & \boldsymbol{\beta}' & \mathbf{s}' & \mathbf{m}' & \mathbf{h}'\end{bmatrix}$, then $\tilde{\mathbf{C}}_{ss}$, $\tilde{\mathbf{C}}_{mm}$, $\tilde{\mathbf{C}}_{sm}$ and $\tilde{\mathbf{C}}_{hh}$ represent the sire by sire, MGS by MGS, sire by MGS and HYS by HYS portions, respectively, of

$$\tilde{\mathbf{C}} = \left(-\frac{\partial^2 \log p\left(\boldsymbol{\theta} \mid \sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2, \mathbf{y}\right)}{\partial\boldsymbol{\theta}\partial\boldsymbol{\theta}'}\right)^{-1}$$

and $\hat{\boldsymbol{\theta}}' = \begin{bmatrix}\hat{\boldsymbol{\tau}}' & \hat{\boldsymbol{\beta}}' & \hat{\mathbf{s}}' & \hat{\mathbf{m}}' & \hat{\mathbf{h}}'\end{bmatrix}$ is the joint maximizer of the conditional posterior density $p\left(\boldsymbol{\theta} \mid \sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2, \mathbf{y}\right)$, readily determined using scoring methods as presented by Gianola and Foulley (1983). In our study, Newton Raphson was used to compute $\hat{\boldsymbol{\theta}}$ based on Fortran90 program that implemented FSPAK90 (Misztal and Perez-Enciso 1998) due to the dimension and sparsity of $\tilde{\mathbf{C}}$.

At convergence, the resulting MML estimates are asymptotically considered to be joint maximizers of $p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right)$, the joint posterior density of the variance/covariance components. Convergence was determined to occur when the absolute difference in all MML estimates from one iterate to the next was less than 10^{-6}. Further details and examples on the implementation of this MML technique invoking EM in animal breeding can be found in Foulley et al. (1987) and Hoeschele et al. (1987).

Laplace's Method

Laplace's method was the second approximate MML technique applied to the data. Details on implementing Laplace's method for variance component estimation in generalized linear mixed models are provided in Tempelman and Gianola (1993) and in Tempelman (1998). Applied to the problem at hand, Laplace's method is based on maximizing the following approximate log marginal joint density of the (co)variance components.

$$\log p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right) \approx \sum_{i=1}^{n} \ln\left(\Phi\left(\tau_{y_i} - \mathbf{x}_i'\hat{\boldsymbol{\beta}} - \mathbf{z}_{1i}'\hat{\mathbf{s}} - \mathbf{z}_{2i}'\hat{\mathbf{m}} - \mathbf{z}_{3i}'\hat{\mathbf{h}}\right) - \Phi\left(\tau_{y_i - 1} - \mathbf{x}_i'\hat{\boldsymbol{\beta}} - \mathbf{z}_{1i}'\hat{\mathbf{s}} - \mathbf{z}_{2i}'\hat{\mathbf{m}} - \mathbf{z}_{3i}'\hat{\mathbf{h}}\right)\right)$$

$$-\frac{q_a}{2}\ln(\mathbf{G}_o) - \frac{[\hat{\mathbf{s}}' \quad \hat{\mathbf{m}}']\mathbf{G}^{-1}\begin{bmatrix}\hat{\mathbf{s}} \\ \hat{\mathbf{m}}\end{bmatrix}}{2} - \frac{q_h}{2}\ln(\sigma_h^2) - \frac{\hat{\mathbf{h}}'\hat{\mathbf{h}}}{2\sigma_h^2} - \frac{1}{2}\ln\left|\tilde{\mathbf{C}}\right| \tag{5}$$

where n is the total number of observations. The MML estimates of the variance components that jointly maximize (5) were determined using the simplex algorithm (Nelder and Mead 1965), as previously implemented for derivative free REML (Meyer 1989). Convergence was assumed when the variance of the values of $\log p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right)$ in the simplex was less than 10^{-6}. In order to control the probability of converging to a local maximum, the simplex algorithm was restarted once from the first set of converged estimates.

Smith and Graser (1986) presented a method for deriving asymptotic standard errors of variance components for derivative-free REML that could be adopted in Laplace's method, doing so jointly for all variance components. We determined this joint assessment to be numerically unstable for our problem. Therefore, approximate standard errors of the Laplace MML estimates were derived separately for each component by holding each of the other components equal to their MML estimates in $\log p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right)$ and profiling $\log p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right)$ over a grid of values for the component of interest. Specifically, a second order polynomial was fitted to this surface in the following manner:

$$b_0 + b_1\sigma_r^2 + b_2\left(\sigma_r^2\right)^2 = \log p\left(\sigma_r^2 \mid \hat{\sigma}_{-r}^2, \mathbf{y}\right) \qquad (6)$$

where $\hat{\sigma}_{-r}^2$ denotes the MML estimates of all variance components other than the component σ_r^2 (r= s, m, sm and h) of current interest. The function in (6) was fitted using 10 equally spaced values of σ_r^2 local to each MML estimate $\hat{\sigma}_r^2$ such that the corresponding asymptotic standard errors was computed as $\left(\sqrt{-2b_2}\right)^{-1}$.

Final MAP solutions to $\boldsymbol{\theta}$ were determined by jointly maximizing $p\left(\boldsymbol{\theta} \mid \sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2, \mathbf{y}\right)$ via Newton-Raphson with the variance components set equal to their approximate MML estimates (EM-based method and Laplace's method). Asymptotic standard errors of the MAP estimate of $\mathbf{s}$ were determined as the square roots of the diagonal elements of $\tilde{\mathbf{C}}_{ss}$ evaluated at the MML estimates of the variance components.

Formal hypothesis testing was carried out on each (co)variance component. Likelihood ratio tests for σ_{sm} and for σ_h^2 were based on computing the difference between $-2\log p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right)$ evaluated at the joint MML estimates with $-2\log p\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2 \mid \mathbf{y}\right)$ maximized with respect all (co)variance components except the parameter(s) of interest which were set to 0. The difference involving σ_{sm} was compared to a χ_1^2 whereas the difference involving σ_h^2 was compared to an equal mixture of χ_0^2 and χ_1^2 as required by Stram and Lee (1994). The likelihood ratio test for testing H$_0$: σ_s^2 = 0 was based on comparing the difference between $-2\log p\left(\sigma_s^2,\sigma_m^2,\sigma_{sm},\sigma_h^2 \mid \mathbf{y}\right)$ evaluated at the joint MML estimates with $-2\log p\left(\sigma_s^2=0,\sigma_m^2,\sigma_{sm}=0,\sigma_h^2 \mid \mathbf{y}\right)$ maximized with respect to σ_h^2 and σ_m^2 against a distribution based on a equal mixture of χ_1^2 and χ_2^2 (Stram and Lee 1994). The hypothesis test H$_0$: σ_m^2 = 0 was similarly tested by determining the difference between $-2\log p\left(\sigma_s^2,\sigma_m^2,\sigma_{sm},\sigma_h^2 \mid \mathbf{y}\right)$ evaluated at the joint MML estimates with $-2\log p\left(\sigma_s^2,\sigma_m^2=0,\sigma_{sm}=0,\sigma_h^2 \mid \mathbf{y}\right)$ maximized with respect to σ_h^2 and σ_s^2.

Markov Chain Monte Carlo (MCMC)

The same model was considered here as with the approximate MML/MAP procedures previously outlined. The same MCMC procedures as outlined by Albert and Chib (1993) and adapted to animal breeding by Sorensen et al. (1995) were applied here with one important exception. The threshold parameters in $\boldsymbol{\tau}$ were sampled jointly using the multivariate Metropolis-Hastings (MH) update presented by Cowles (1996). In agreement with the simulation studies by Cowles (1996), the Cowles MH update facilitated considerably faster mixing on the threshold parameters relative to sampling from univariate full conditionals on τ_2 and τ_3, as presented by Albert and Chib (1993). This issue is not trivial since the slowest mixing parameters in previous MCMC threshold model analyses are generally the threshold parameters (Sorensen et al. 1995; Varona et al. 1999). Flat priors were invoked on the fixed effects and on the variance components.

Three separate MCMC chains of 85,000 cycles were generated. Starting values for parameters in chain 1 were based on Laplace estimates of variance components. In chain 2, starting values were set equal to each Laplace variance component estimate plus three times the corresponding asymptotic standard error whereas for chain 3, starting values were set equal to each Laplace variance component estimate minus three times the corresponding asymptotic standard error. After discarding the first 5,000 cycles within each chain as "burn-in" (Gelman and Rubin, 1992), each set of the remaining 80,000 cycles within each chain were subsequently saved to determine the marginal posterior density of each variance component and identifiable threshold parameters and to determine the posterior means and standard deviations of each location parameter.

Generally, MCMC implementations are most problematic for variance component and threshold parameters in terms of convergence and mixing (Sorensen et al. 1995). Convergence diagnostics were assessed for each variance component and threshold parameters by computing the potential scale reduction factor $\hat{R}$ of Gelman and Rubin (1992) throughout burn-in. This diagnostic is based on an ANOVA technique that computes the ratio of between chain variability to within chain variability, and which should approach 1 at convergence. The effectiveness of MCMC mixing after burn-in was determined by effective sample size (ESS) of the samples (Sorensen et al. 1995; Hoeschele and Tier 1995) using the initial positive sequence estimator (Geyer 1992). The ESS is an estimate on the information content of the MCMC samples in terms of an equivalent number of independent samples.

Inference on Heritabilities and Genetic Correlations

Point estimates and posterior densities of the additive direct variance σ_D^2, additive maternal σ_M^2 variances, and the corresponding direct-maternal covariance σ_{DM} can be derived from σ_s^2, σ_m^2 and σ_{sm} (Manfredi et al. 1991a,b; Matos et al. 1994; Luo et al. 1999), using

$$\begin{bmatrix} \sigma_D^2 \\ \sigma_{DM} \\ \sigma_M^2 \end{bmatrix} = \begin{bmatrix} 4 & 0 & 0 \\ -2 & 4 & 0 \\ 1 & -4 & 4 \end{bmatrix} \begin{bmatrix} \sigma_s^2 \\ \sigma_{sm} \\ \sigma_m^2 \end{bmatrix} \tag{7}$$

The phenotypic variance (σ_P^2) is defined by

$$\sigma_P^2 = \sigma_s^2 + 2\sigma_{sm} + \sigma_m^2 + \sigma_h^2 + \sigma_e^2 \tag{8}$$

Inferences on additive direct (h_D^2) and maternal (h_M^2) heritabilities and the direct-maternal genetic correlation (r_{DM}) were further determined using the following relationships: $h_D^2 = \frac{\sigma_D^2}{\sigma_P^2}$, $h_M^2 = \frac{\sigma_M^2}{\sigma_P^2}$ and $r_{DM} = \frac{\sigma_{DM}}{\sqrt{\sigma_D^2 \sigma_M^2}}$. Note that with HYS treated as random and hence σ_h^2 included as part of σ_P^2, the heritabilities estimated in this study are effectively reported as "across-herd" heritabilities rather than as "within-herd" heritabilities as would be for the case when HYS are treated as fixed.

RESULTS AND DISCUSSION

Assessment of MCMC Convergence and Mixing

Based on the raw trace plots of samples from 85,000 cycles and Gelman and Rubin's $\hat{R}$ computed from the 3 chains, it was determined that 5,000 cycles was a sufficiently long burn-in period for all dispersion and threshold parameters and within all chains; i.e., the length of the burn-in period was enough to eliminate the effect of the different starting values. The $\hat{R}$ values for the slowest mixing parameters (variance components and threshold parameters) were all equal to 1.00 by the end of the burn-in period.

The estimated ESS for each variance component and threshold parameter is given in Table I and is based on a sum of separate determinations from each of the three separate chains. The ESS for these parameters ranged from 1,705 to 6,953, indicating sufficient MCMC mixing. Several animal breeders have recently suggested 100 as the minimum ESS for reliable statistical inference (Uimari et al. 1996; Bink et al. 1998). The ESS of 3,211 and 3,110 for τ_2 and τ_3 were found to be higher than that for the variance components and considerably higher than what has been determined for threshold parameters in comparable MCMC studies (Varona et al. 1999; Luo et al. 2001). Again, improved mixing was most likely due to the Cowles MH update.

Variance Component Inference

Point estimates of variance components based on MML using EM, Laplace's method and based on posterior means, modes and medians using MCMC are given in Table II. The median has been suggested (Raftery and Lewis 1992) as a more robust point estimator compared to the posterior mean. However, this study demonstrated no appreciable differences between the posterior mean, mode, and median of parameters since the posterior distributions of variance components and threshold parameters were nearly symmetric. The point estimates from the three independent MCMC chains were, as expected, highly repeatable (not shown) because of the individually large ESS.

In this study, the EM-MML method produced slightly lower point estimates of variance components compared to the Laplace MML method, which in turn lead to slightly lower estimates relative to any of the MCMC point estimates. These results are in agreement with what was anticipated given the simulation study results of Tempelman (1998). That is, genetic variance estimates based on the use of the EM-MML method may be slightly biased downwards. Nevertheless, there appeared to be no significant difference in these estimates between all three methods in this study.

All likelihood ratio tests (test statistics not presented) based on Laplace's method indicated that all components of variance and covariance $\left(\sigma_s^2, \sigma_m^2, \sigma_{sm}, \sigma_h^2\right)$ were statistically significant (P<0.0001). Furthermore, the asymptotic standard errors of the Laplace MML estimates closely corresponded to the posterior standard deviations determined using MCMC, thereby suggesting that the joint posterior density of the variance components was close to being multivariate normal. Further evidence of this is indicated by the 95% posterior probability intervals being nearly symmetric about the respective posterior means.

Table II also indicates that maternal genetic variability for calving difficulty is appreciable in Piemontese cattle. However, there was no evidence to support a non-zero additive-maternal covariance.

Heritabilities and Genetic Correlations

Inferences on direct and maternal heritabilities and the genetic correlation are presented in Table II. Point estimates of the heritabilities and genetic correlation obtained from the MCMC algorithm were similar across all chains and estimation methods (posterior mean, mode and median). These results indicated that the posterior distributions of genetic parameters were nearly symmetric. As with the variance components, the EM-MML estimates were found to be slightly lower than the Laplace MML estimates and the various MCMC point estimates.

Our heritability estimates were similar to findings of Varona et al. (1999) who used a threshold animal model with direct and maternal effects, but they were substantially higher than the threshold model estimates reported by Manfredi et al. (1991a,b), McGuirk et al. (1998), McGuirk et al. (1999), Luo et al. (1999), and Bennett and Gregory (2001). The genetic correlation did not appear to be statistically significant; nevertheless, the 95% posterior probability interval was extensive (i.e. from -0.29 to 0.25). In contrast, significantly negative direct-maternal genetic correlations have been reported using threshold models (Luo et al. 1999; Bennett and Gregory 2001) and linear models (Carnier et al. 2000) for the analysis of calving ease.

Carnier et al. (2000) used a linear mixed model to analyze a data set from a source virtually identical to that used in this study and reported lower heritability estimates and a significantly negative genetic correlation estimate compared to estimates reported in Table II. In field data studies of various categorical traits in animal breeding, Weller et al. (1988), Olsen et al. (1994), Matos et al. (1997), Varona et al. (1999) also found that linear model heritability estimates were smaller than threshold model heritability estimates, as anticipated from theory (Dempster and Lerner 1950). Our results suggest that selection of sires for calving ease of their progeny should not result in antagonistic maternal effects over successive generations. The differences in results from Carnier et al. (2000) may be based on model specification (i.e. threshold sire and maternal grandsire versus linear animal model; fixed versus random HYS effects) and substantial differences in data editing. Nearly twice as many records were used by Carnier et al. (2000) whereas the current study concentrated on herds having 50 or more records over the same time period. To investigate the impact of the HYS specification further, data were analyzed with two linear mixed (sire-maternal grandsire) models, treating HYS as fixed in one case and as random in the other. Treating HYS as fixed in a threshold mixed model was not feasible due to the extreme category problem (Hoeschele and Tier 1995). A statistically significant genetic estimate of -0.72 was found with fixed HYS effects whereas a nonsignificant genetic correlation estimate of -0.05 was estimated when HYS were treated as random. This implies that the direct-maternal genetic covariance may be heterogeneous across different environments (i.e. different herds) and particularly influenced by herd size since fixed versus random HYS specifications should lead to similar results for large herds.

Comparison of Inferences on Sire Effects

Empirical Bayes or MAP estimates of sire effects were computed by maximizing the joint density of fixed and random effects conditioned upon estimated variance components by EM and Laplacian algorithms; the respective MAP sire effect estimates are labeled MAP-EM and MAP-Laplace. Posterior means of solutions were determined to be corresponding point estimates of sire effects using MCMC. The Pearson and rank correlations between these estimates were computed and found to be greater than 0.99 between MAP-EM and MAP-Laplace, between MAP-EM and MCMC, and between MAP-Laplace and MCMC; i.e. there were no substantial differences in ranking. A simple linear regression involving estimated sire effects of MCMC on MAP-EM, MCMC on MAP-Laplace and MAP-Laplace on MAP-EM indicating regression slope estimates only slightly different from one, respectively, 1.06, 1.03 and 1.03. Wang et al. (1997) illustrated a similar relationship in a simulation study whereby the regression coefficient of MAP on MCMC-derived posterior means for direct genetic effects was slightly greater than one, 1.08. They also determined the corresponding correlation to be high (>0.99).

Posterior standard errors of the sire effects can be used to derive approximate accuracies of estimated genetic merits. These standard errors were determined as the standard deviation of the samples from MCMC and from the square root of the diagonals of $\mathbf{C}_{ss}$, based on both EM and Laplace estimates of variances. Simple linear regression analyses of these standard errors based on MCMC versus MAP-EM, MCMC versus MAP-Laplace and MAP-Laplace versus MAP-EM, resulted in intercepts not different from 0 but estimated slopes of 1.09, 1.03, and 1.07, respectively, indicating that the posterior standard errors were on average larger under MCMC than under MAP estimates. This was anticipated as uncertainty on the variance components is accounted for in fully marginal inference using MCMC but not so in MAP. In all cases, the correlation between the estimated standard errors was near one.

CONCLUSIONS

In spite of the results of several smaller simulation studies, our work showed that there were no appreciable differences between approximate MML/MAP versus MCMC methods for inferences on genetic parameters and genetic merit on calving ease under a threshold sire and maternal grandsire model and derived from a relatively large data set. Furthermore, MCMC mixing was substantially improved relative to previously published implementations due to the use of a joint MH update for the threshold parameters. Maternal genetic variation was estimated to be an important source of variability although the genetic correlation between direct and maternal effects was not significant. The impact of random versus fixed HYS effects on the estimates of this genetic correlation warrants further study.

Hence, there does not appear to be a pressing need to use MCMC methods for national genetic evaluations of calving ease based on conventionally specified threshold and maternal grandsire sire models. However, this may not be true for animal model specifications.

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Table I. Effective sample sizes for (co)variance components and threshold parameters using MCMC for first parity calving ease scores in Piemontese cattle.

	PARAMETER					
	σ_s^2	σ_m^2	σ_{sm}	σ_h^2	τ_2	τ_3
ESS[a]	1,799	1,705	1,799	6,953	3,211	3,110

[a]The combined effective sample sizes based on the sum of determinations from 3 independent MCMC chains post burn-in, each based on 80,000 samples.

Table II. Estimation of variance-covariance components and genetic parameters for calving difficulty in Piemontese cattle using EM, Laplacian, and MCMC algorithms.

Variance component	EM[a]	Laplace[b]	MCMC			
			PM[c]	PMD[d]	PME[e]	PPI[f]
σ_s^2	0.083	0.091±0.011	0.095±0.014	0.093	0.095	0.070-0.123
σ_m^2	0.055	0.060±0.008	0.064±0.010	0.062	0.062	0.046-0.084
σ_{sm}	0.041	0.045±0.007	0.045±0.008	0.044	0.044	0.029-0.061
σ_h^2	0.185	0.208±0.013	0.217±0.013	0.217	0.217	0.192-0.243
σ_D^2	0.331	0.363	0.380±0.055	0.373	0.373	0.278-0.493
σ_M^2	0.140	0.151	0.170±0.037	0.163	0.163	0.106-0.252
σ_{DM}	-0.002	-0.002	-0.011±0.035	-0.011	-0.011	-0.084-0.055
h_D^2	0.236	0.251	0.259±0.0348	0.253	0.258	0.194-0.330
h_M^2	0.100	0.105	0.116±0.0256	0.112	0.114	0.072-0.173
r_{DM}	-0.008	-0.009	-0.034±0.136	-0.051	-0.037	-0.292-0.245

[a] Joint MML estimates using EM algorithm.

[b] Joint MML estimates using Laplace algorithm ± asymptotic standard error.

[c] Posterior mean ± posterior standard deviation.

[d] Marginal posterior mode.

[e] Marginal posterior median.

[f] 95% posterior probability interval.

CHAPTER 3

An Assessment of Cumulative *t*-Link Threshold Models for the Quantitative Genetic Analysis of Calving Ease Scores

ABSTRACT

The Student-*t* and other heavy-tailed distributions have been specified for residuals to facilitate robust statistical inference in linear mixed models. In this study, we develop a hierarchical threshold mixed model based on a cumulative *t*-link specification for the analysis of ordinal data, specifically, calving ease scores. The validation of our model and our Markov Chain Monte Carlo (MCMC) algorithm was carried out on simulated data from normally and t_4 (i.e. a *t* distribution with 4 degrees of freedom) distributed populations using the deviance information criterion (DIC) and a related measure to validate recently proposed model choice criteria. The simulation study indicated that although inference on the degrees of freedom parameter is possible, MCMC mixing was problematic. Nevertheless, the DIC was shown to be a satisfactory measure of model fit to data. We applied a sire maternal and grandsire cumulative *t*-link model to a calving ease dataset from 8,847 Italian Piemontese first parity dams. The cumulative t_4-link model was shown to lead to posterior means of direct and maternal heritabilities (0.40±0.06, 0.11±0.04) and a direct maternal genetic correlation (-0.58±0.15) that were not different from the corresponding posterior means of the heritabilities (0.42±0.07, 0.14±0.04) and the genetic correlation (-0.55±0.14) inferred under the conventional cumulative probit link threshold model. Furthermore, the correlation (>.99) between posterior means of sire progeny merit from the two models

suggested no meaningful rerankings. Nevertheless, the cumulative *t*-link model was decisively chosen as the better fitting model using DIC.

INTRODUCTION

Data quality is an increasingly important issue for genetic evaluation of livestock, both from a national and international perspective (Emanuelson *et al.* [13]). Breed associations and government agencies typically invoke arbitrary data quality control edits in order to minimize the impact of recording error, preferential treatment and/or injury/disease on predicted breeding values (Bertrand and Wiggans [4]) in the belief that the data residuals should be normally distributed.

It has been recently demonstrated that the specification of Student *t* distributed residuals in linear mixed models may effectively mute the impact of residual outliers, particularly in situations where preferential treatment of some breedstock may be anticipated (Stranden and Gianola [38]). Based on the work of Lange *et al.* [22] and others, Stranden and Gianola [39] developed the corresponding hierarchical Bayesian models for animal breeding, using Markov Chain Monte Carlo (MCMC) methods for inference. In their models, residuals were specified as either having independent (univariate) *t* distributions or multivariate *t* distributions within herd clusters. Outside of possibly longitudinal studies, the multivariate specification is of dubious merit ([32], [38], [39]) such that all of our subsequent discussion pertains to the univariate specification only.

A Student *t* distribution can be represented as a scale mixture of normals with Gamma distributed scaling factors (Lange *et al.* [22]). Alternative specifications of scale mixture of normals, all of which lead to heavy-tailed residual densities relative to the normal, are further considered by Carlin and Polson [6] and in an animal breeding context by Rosa [32]. Using Bayes factors approximations, Rosa [32] noted that these heavier tailed models provided better fits to a dataset on birth weights in rats than a model based on a Gaussian error distribution. More recent applications include linkage mapping of quantitative trait loci (von Rohr and Hoeschele [44]).

Auxiliary traits such as calving ease or milking speed are often subjectively scored on an ordinal scale. It might then be anticipated that data quality would be an issue of greater concern in these traits than more objectively measured production characters, particularly since record keeping is generally unsupervised, being the responsibility of the attending herdsperson. Luo *et al.* [23] has suggested that a decline in the diligence of data recording was partially responsible for their lower heritability estimates of calving ease relative to earlier estimates from the same Canadian Holstein population.

The cumulative probit link (CP) generalized linear mixed model, otherwise called the threshold model, is currently the most commonly used genetic evaluation model for calving ease ([3, 46]). MCMC methods are particularly well suited to this model since the augmentation of the joint posterior density with normally distributed underlying or latent liability variables facilitate implementations very similar to those developed for linear mixed effects models ([1, 36]). A cumulative *t* link (CT) model has been proposed by Albert and Chib [1] for the analysis of ordinal categorical data, thereby providing greater modeling flexibility relative to the CP model. The CT model can be created by simply augmenting the joint posterior density with *t*-distributed rather than normally distributed underlying liability variables based on a Gamma scale mixture of normals.

The objectives of this study were to validate MCMC inference of the CT generalized linear mixed (sire) model via a simulation study and to compare the fit of this model with the CP model for the quantitative genetic analysis of calving ease scores in Italian Piemontese cattle.

MODEL CONSTRUCTION

Suppose that elements of the *n* x 1 data vector $\mathbf{Y} = \{Y_i\}_{i=1}^{n}$ can take values in any one of *C* mutually exclusive ordered categories. The classical CP model for ordinal data (Gianola and Foulley [17]) can be written as follows:

$$\operatorname{Prob}\left(Y_i = j \mid \boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\tau}\right) = \Phi\left(\frac{\tau_j - \left(\mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}\right)}{\sigma_e}\right) - \Phi\left(\frac{\tau_{j-1} - \left(\mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}\right)}{\sigma_e}\right), \tag{1}$$

where $j = 1,2,\ldots,C$ denotes the index for categories. Also $\Phi(.)$ denotes the standard normal cumulative distribution function, $\boldsymbol{\beta}$ and $\mathbf{u}$ are the vectors of unknown fixed and random effects, and $\boldsymbol{\tau}' = \left[\tau_o \quad \tau_1 \quad \ldots \quad \tau_C\right]$ is a vector of unknown threshold parameters satisfying $\tau_1 < \tau_2 \ldots < \tau_C$ with $\tau_0 = -\infty$ and $\tau_C = +\infty$. Furthermore, $\mathbf{x}_i'$ and $\mathbf{z}_i'$ are known incidence row vectors. Latent liability variables ($\mathbf{L} = \{L_i\}_{i=1}^{n}$) can be introduced to alternatively define the same specification as in (1) but in two hierarchical stages:

$$\operatorname{Prob}\left(Y_i = j \mid L_i, \boldsymbol{\tau}\right) = \sum_{j=1}^{C} 1\left(\tau_{j-1} < L_i < \tau_j\right) 1\left(Y_i = j\right) \tag{2a}$$

$$L_i \mid \boldsymbol{\beta}, \mathbf{u}, \sigma_e^2 \sim N\left(\mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}, \sigma_e^2\right) \tag{2b}$$

for $i = 1,2,\ldots,n$. Here 1(.) denotes an indicator function, which is equal to 1 when the expression in the function is true and is equal to 0 otherwise. As shown by Albert and Chib [1] and in an animal breeding context by Sorensen *et al.* [36]; this introduction of **L** facilitates a tractable MCMC implementation.

The CT model is a generalization of (1), that is,

$$\text{Prob}\left(Y_i = j \mid \boldsymbol{\beta},\mathbf{u},\boldsymbol{\tau},v,\sigma_e^2\right) = F_v\left(\frac{\tau_j - \left(\mathbf{x}_i'\boldsymbol{\beta}+\mathbf{z}_i'\mathbf{u}\right)}{\sigma_e}\right) - F_v\left(\frac{\tau_{j-1} - \left(\mathbf{x}_i'\boldsymbol{\beta}+\mathbf{z}_i'\mathbf{u}\right)}{\sigma_e}\right) \tag{3}$$

for $j = 1,2,\ldots,C$ where F_v represents the cumulative density function of a standard Student t-distribution with degrees of freedom v. Note that as $v \rightarrow \infty$, (3) $\rightarrow$ (1) such that the standard CP model is simply a special case of the CT model. Like the CP model, the CT model can also be represented as a two-stage specification, with the first stage as in (2a) but the second stage specified as:

$$p\left(L_i \mid \boldsymbol{\beta},\mathbf{u},\sigma_e^2,v\right) = \frac{\Gamma\left(\frac{v+1}{2}\right)}{\Gamma\left(\frac{v}{2}\right)\Gamma\left(\frac{1}{2}\right)\left(v\sigma_e^2\right)^{\frac{1}{2}}}\left(1+\frac{\left(L_i-\left(\mathbf{x}_i'\boldsymbol{\beta}+\mathbf{z}_i'\mathbf{u}\right)\right)^2}{v\sigma_e^2}\right)^{-\frac{1}{2}(v+1)}, \tag{4}$$

i.e., L_i is Student t-distributed with location parameter $\mu_i = \mathbf{x}_i'\boldsymbol{\beta}+\mathbf{z}_i'\mathbf{u}$, scale parameter $\sigma_e^2>0$ and degrees of freedom $v>0$ for $i=1,2,\ldots,n$. In turn, equation (4) can be represented by a two-stage scale mixture of normals:

$$L_i \mid \boldsymbol{\beta},\mathbf{u},\sigma_e^2,\lambda_i \sim N\left(\mathbf{x}_i'\boldsymbol{\beta}+\mathbf{z}_i'\mathbf{u},\frac{\sigma_e^2}{\lambda_i}\right) \tag{5a}$$

$$p(\lambda_i \mid v) = \frac{\left(\frac{v}{2}\right)^{\frac{v}{2}}}{\Gamma\left(\frac{v}{2}\right)}\lambda_i^{\frac{v}{2}-1}\exp\left\{-\frac{\lambda_i}{2}v\right\} \tag{5b}$$

Note that (5b) specifies a Gamma density with parameters $v/2$ and $v/2$, thereby having an expectation of 1. The remaining stages of our hierarchical model are characteristic of animal breeding models. We write

$$\boldsymbol{\beta} \sim p(\boldsymbol{\beta}) \tag{6}$$

where $p(\boldsymbol{\beta})$ is a subjective prior, typically specified to be flat or vaguely informative. Furthermore, the random effects are typically characterized by a structural multivariate prior specification:

$$\mathbf{u}|\boldsymbol{\varphi} \sim p(\mathbf{u}|\boldsymbol{\varphi}) \sim N(\mathbf{0},\mathbf{G}(\boldsymbol{\varphi})) \tag{7}$$

Here $\mathbf{G}(\boldsymbol{\varphi})$ is a variance-covariance matrix that is a function of several unknown variance components or variance-covariance matrices in $\boldsymbol{\varphi}$, depending on whether or not there are multiple sets of random effects and/or specified covariances between these sets; an example of the latter is the covariance between additive and maternal genetic effects. Furthermore, flat priors, inverted Gamma densities, inverted Wishart densities or products thereof may be specified for the prior density $p(\boldsymbol{\varphi})$ on $\boldsymbol{\varphi}$, depending, again, on the number of sets of random effects and whether there are any covariances thereof (Jensen *et al.* [20]).

Finally, a prior is required for the degrees of freedom parameter v. We use the prior

$$p(v) \propto \frac{1}{(1+v)^2} \tag{8}$$

which is consistent with a Uniform(0,1) prior on $1/(1+v)$.

As with CP models, there are identifiability issues involving elements of $\boldsymbol{\tau}$ with σ_e^2 such that constraints are necessary. Typically, one element of $\tau_1, \tau_2, \ldots, \tau_{C-1}$ is restricted to an arbitrary value (e.g. τ_1=0) along with $\sigma_e^2 = 1$. This is the parameterization we chose such that inference on σ_e^2 is not subsequently considered in this paper.

Presuming that the elements of **Y** are conditionally independent given $\boldsymbol{\beta}$ and **u**, we can write the joint posterior density of all unknown parameters and latent variables (**L**) as follows:

$$p(\boldsymbol{\beta},\mathbf{u},\boldsymbol{\tau},\boldsymbol{\varphi},\nu,\mathbf{L},\boldsymbol{\lambda}\mid\mathbf{y}) \\ \propto\left(\prod_{i=1}^{n}\text{Prob}(y=y_i\mid L_i,\boldsymbol{\tau})p\left(L_i\mid\boldsymbol{\beta},\mathbf{u},\sigma_e^2,\lambda_i\right)p(\lambda_i\mid\nu)\right)p(\boldsymbol{\beta})p(\mathbf{u}\mid\boldsymbol{\varphi})p(\boldsymbol{\varphi})p(\nu) \tag{9}$$

where $\boldsymbol{\lambda}=\{\lambda_i\}_{i=1}^{n}$.

A MCMC inference strategy involves determining and generating random variables from the full conditional densities (FCD's) of each parameter or blocks thereof. Many of the FCD's can be directly derived using results from Sorensen *et al.* [36] jointly with results from Stranden and Gianola [39]. Let $\boldsymbol{\theta}=[\boldsymbol{\beta}'\ \mathbf{u}']'$. It can be readily shown that the FCD of $\boldsymbol{\theta}$ is multivariate normal:

$$\boldsymbol{\theta}\mid\mathbf{y},\nu,\boldsymbol{\lambda},\mathbf{L}\sim N\left(\hat{\boldsymbol{\theta}},\mathbf{W}'\mathbf{R}^{-1}\mathbf{W}+\boldsymbol{\Sigma}^{-}\right) \tag{10}$$

where $\mathbf{R}^{-1}=diag\{\lambda_i\}_{i=1}^{n}$ is a diagonal matrix, $\boldsymbol{\Sigma}^{-}=\begin{bmatrix}\mathbf{0}_{pxp} & \mathbf{0}_{pxq}\\ \mathbf{0}_{qxp} & \left(\mathbf{G}(\boldsymbol{\varphi})\right)^{-1}\end{bmatrix}$, $\mathbf{W}=[\mathbf{X}\quad\mathbf{Z}]$ for

$\mathbf{X}=[\mathbf{x}_1\quad\mathbf{x}_2\quad\ldots\quad\mathbf{x}_n]'$, $\mathbf{Z}=[\mathbf{z}_1\quad\mathbf{z}_2\quad\ldots\quad\mathbf{z}_n]'$, and

$$\hat{\boldsymbol{\theta}}=\begin{bmatrix}\hat{\boldsymbol{\beta}}\\ \hat{\mathbf{u}}\end{bmatrix}=\left[\mathbf{W}'\mathbf{R}^{-1}\mathbf{W}+\boldsymbol{\Sigma}^{-}\right]^{-1}\mathbf{W}'\mathbf{R}^{-1}\mathbf{L} \tag{11}$$

Generation of individual elements θ_j, j=1,2,...,p+q or blocks thereof of $\boldsymbol{\theta}$ from their respective FCD is straightforward using the strategy presented by Wang *et al.* [45].

The FCD of individual elements of **L** and $\boldsymbol{\tau}$ are straightforward to generate from using results from Sorensen *et al.* [36]. We, however, prefer the Metropolis-Hastings and method of composition joint update of **L** and $\boldsymbol{\tau}$ presented by Cowles [11]. She demonstrated and we have further noted in our previous applications (Kizilkaya *et al.* [21]) that the resulting MCMC mixing properties using this joint update are vastly superior to using separate Gibbs updates on individual elements of **L** and $\boldsymbol{\tau}$ as outlined by Sorensen *et al.* [36].

If some partitions of $\boldsymbol{\varphi}$ form a variance-covariance matrix, then their respective FCD can be readily shown to be inverted-Wishart (Jensen *et al.* [20]) whereas if other partitions of $\boldsymbol{\varphi}$ involve scalar variance but no covariance components, then the FCD of each component can be shown to be inverted-gamma.

The FCD of λ_i can be shown to be

$$p(\lambda_i \mid \boldsymbol{\lambda}_{-i}, \mathbf{L}, \boldsymbol{\theta}, \nu) \propto \lambda_i^{\left(\frac{\nu+1}{2}\right)-1} \times \exp\left(-\frac{\lambda_i}{2}\left(\left(L_i - \mathbf{x}_i'\boldsymbol{\beta} - \mathbf{z}_i'\mathbf{u}\right)^2 + \nu\right)\right) \tag{12}$$

that is, the kernel in (12) specifies that distribution to be

$\text{Gamma}\left(\frac{\nu+1}{2}, \frac{1}{2}\left(\nu + \left(L_i - \mathbf{x}_i'\boldsymbol{\beta} - \mathbf{z}_i'\mathbf{u}\right)^2\right)\right)$. Here $\boldsymbol{\lambda}_{-i}$ denotes all elements of $\boldsymbol{\lambda} = \{\lambda_i\}$ except for λ_i, i = 1,2,....n.

Finally, the FCD of ν can be shown to be

$$p(\nu \mid \boldsymbol{\beta}, \mathbf{u}, \mathbf{L}, \boldsymbol{\lambda}) \propto \left(\frac{\left(\frac{\nu}{2}\right)^{\nu/2}}{\Gamma(\nu/2)}\right)^n \left(\prod_{i=1}^{n} \lambda_i^{\frac{\nu}{2}-1} \exp\left(-\frac{\nu}{2}\lambda_i\right)\right) \frac{1}{(1+\nu)^2} \tag{13}$$

given the specification for $p(v)$ in (8). Equation (13) is not a recognizable density such that a Metropolis-Hastings update is required. We utilized a random walk implementation (Chib and Greenberg [10]) of Metropolis-Hastings sampling; specifically, a normal density with expectation equal to the parameter value from the previous MCMC cycle was used as the proposal density for drawing from the FCD of $\kappa = \log(v)$, using equation (13) and the necessary Jacobian for this transformation. The Metropolis-Hastings acceptance ratio was tuned to intermediate rates (40-50%) during the MCMC burn-in period to optimize MCMC mixing (Chib and Greenberg [10]). Since the variance of a *t*-density is not defined for $v \leq 2$, we truncate sampled from (13) such that $v > 2$, or equivalently $\kappa > \log(2)$.

MODEL COMPARISON

Model choice is an important issue that has not received considerable attention in animal breeding until only very recently ([19, 31]). Likelihood ratio tests have been used to compare differences in fit between various models and their reduced subsets; however, these tests do not facilitate more general model comparisons. The Bayes factor has a strong theoretical justification as a general model choice criterion; however algorithms for Bayes factors computations are either computationally intensive (e.g. Chib [9]) or numerically unstable (Newton and Raftery [30]). Furthermore, as Gelfand and Ghosh [15] indicate, Bayes factors lack clear interpretation in the case of improper priors which are particularly frequent specifications in animal breeding hierarchical models. Akaike's information criterion or Schwarz's Bayesian criterion are analytical measures that provide an asymptotic representation of Bayes factors and reflect a compromise between goodness of fit and number of parameters. As the total number of parameters and latent variables often exceeds the number of observations in an animal breeding (e.g. animal model) analysis, the effective number of parameters in hierarchical models is not always so obvious. The MCMC sample average of the posterior log likelihoods, or data sampling log densities, may be used as a means for comparing different models (Dempster [12]); however, as Speigelhalter *et al.* [37] indicate, it is not always so obvious how to proceed when these densities are similar but the number of parameters and/or the numbers of hierarchical stages of the candidate models vary. Speigelhalter *et al.* [37] proposed the deviance information criterion (DIC) for comparing alternative constructions of hierarchical models. The DIC is based on the posterior distribution of the deviance statistic, which is -2 times the sampling distribution of the data as specified in the first stage of a hierarchical model. It may not be so obvious, however, what exactly the data sampling stage is in a hierarchical model. For example, the data sampling stage for the CT model may be specified in one way as

$$\text{Prob}\left(Y_i = j \mid \boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\tau}, \lambda_i, \sigma_e^2\right) = \Phi\left(\frac{\tau_j - \left(\mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}\right)}{\frac{\sigma_e}{\sqrt{\lambda_i}}}\right) - \Phi\left(\frac{\tau_{j-1} - \left(\mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}\right)}{\frac{\sigma_e}{\sqrt{\lambda_i}}}\right) \qquad (14)$$

given the specifications of (2a) and (5a) or it may be specified more marginally using (3). We prefer a more marginalized or heavier-tailed first stage specification such as (3) for CT and (1) for CP, potentially leading to a more stable implementation with justification provided by Satagopan *et al.* [34] but with their context being the stabilization of the Bayes factor estimator of Newton and Raftery [30].

The DIC is computed as the sum of average Bayesian deviance ($\bar{D}$) plus the "effective number of parameters" (p_D) with respect to a model, such that smaller DIC values indicate better fit to the data. Let G denote the number of cycles after convergence in a MCMC chain. Furthermore, we represent all unknown parameters in the marginalized first stage specification by $\boldsymbol{\vartheta} = (\boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\tau}, v)$ with $\boldsymbol{\vartheta}$ excluding $v=\infty$ in the CP model. Then, for the CT model, then the average Bayesian deviance can be estimated using (3) by

$$\bar{D} = -2\left(\sum_{g=1}^{G}\sum_{i=1}^{n}\log\left(\text{Prob}\left(Y = y_i \mid \boldsymbol{\beta}^{[g]}, \mathbf{u}^{[g]}, \boldsymbol{\tau}^{[g]}, v^{[g]}\right)\right)\right)$$

where the superscript [g] denotes the MCMC cycle g, $g = 1,2,\ldots,G$ for the sampled value of the corresponding parameter. Furthermore, p_D can be estimated as $p_D = \bar{D} - D(\bar{\boldsymbol{\vartheta}})$ where

$$D(\bar{\boldsymbol{\vartheta}}) = -2\left(\sum_{i=1}^{n}\log\text{Prob}\left(Y = y_i \mid \bar{\boldsymbol{\beta}}, \bar{\mathbf{u}}, \bar{\boldsymbol{\tau}}, \bar{v}\right)\right).$$

Here the bar notation (e.g. $\bar{\boldsymbol{\vartheta}}$) denotes the corresponding posterior mean vector.

We alternatively considered the conditional predictive ordinate (CPO) as the basis for model choice (Gelfand [14]). Defined for observation i, we write the CPO as

$$\hat{\pi}(y_i \mid \mathbf{y}_{-i}, \text{M}_1) = \left[\frac{1}{G}\sum_{g=1}^{G}\left(\text{Prob}\left(Y = y_i \mid \boldsymbol{\beta}^{[g]}, \mathbf{u}^{[g]}, \boldsymbol{\tau}^{[g]}\right)\right)^{-1}\right]^{-1}$$

using (1) for the CP model (Model M$_1$) and

$$\hat{\pi}(y_i \mid \mathbf{y}_{-i}, \text{M}_2) \approx \left[\frac{1}{G}\sum_{g=1}^{G}\left(\text{Prob}\left(Y = y_i \mid \boldsymbol{\beta}^{[g]}, \mathbf{u}^{[g]}, \boldsymbol{\tau}^{[g]}, v^{[g]}\right)\right)^{-1}\right]^{-1}$$

using (3) for the CT model (Model M_2). Here $\mathbf{y}_{-i}$ denotes all observations other than y_i. The log marginal likelihood (LML) of the data for a certain model, say M_k, can then be estimated as:

$$LML = L(\mathbf{y} \mid M_k) = \sum_{i=1}^{n} \log\left(\hat{\pi}\left(y_i \mid \mathbf{y}_{-i}, M_k\right)\right)$$

Larger values of LML indicate better model fit to the data.

DATA

Simulation Study

A simulation study was used to validate the CT model and the utility of the DIC and the LML for model choice between CP and CT. Three replicated datasets were generated from each of two different populations as characterized by the distribution of the liability residuals. Population I had a residual density that was standard normal whereas Population II had a residual density that was standard Student-*t* distributed with scale parameter $\sigma_e^2 = 1$ and degrees of freedom $v_e = 4$. All datasets were generated based on a simple random effects (sire) model with null mean. Liability data for 50 progeny from each of 50 unrelated sires was generated by summing independently drawn sire effects from $N(0, \sigma_s^2 = 0.10)$ with independently drawn residuals from $N(0, \sigma_e^2 = 1.00)$ for a total of 2500 records. These underlying liabilities were mapped to ordinal data with four categories based on the threshold parameter values of $\tau_1 = -0.50$, $\tau_2 = 1.00$, and $\tau_3 = 2.00$ for all populations. Ordinal data from each replicated dataset was analyzed using both CP and CT sire models. For purposes of parameter identifiability, we invoked the restrictions $\sigma_e^2 = 1$ and $\tau_1 = -0.50$. As a positive control, the underlying liability data for each replicate was analyzed using both normal and *t* distributed error mixed linear models. For the *t* distributed error model, the MCMC procedure adapted was similar to that presented in Stranden and Gianola [39], except that the degrees of freedom parameter (ν>2) was inferred as a continuous (rather than discrete) parameter, using the Metropolis-Hastings update as presented earlier. Graphical inspection of the chains based on preliminary analyses was used to determine a common length of burn-in period. For each replicated data set within each population, a burn-in period of 20,000 cycles was discarded before saving samples from each of an additional 100,000 MCMC cycles. Furthermore, DIC and LML values were computed for each model on each replicated dataset to validate those measures as model choice criteria. In all cases, flat priors were invoked on the variance components.

Italian Piemontese Calving Ease Data

First parity calving ease scores recorded on Italian Piemontese cattle from January, 1989 to July, 1998 by ANABORAPI (Associazione Nazionale Allevatori Bovini di Razza Piemontese, Strada Trinità 32a, 12061 Carrù, Italy) were used for this study. In order to limit computing demands, only herds that were represented by at least 100 records over that nine-year period were considered for the demonstration of the proposed methods in this paper, leaving a total of 8,847 records. Calving ease was coded into five categories by breeders and subsequently recorded by technicians who visited the breeders monthly. The five ordered categories are: 1) unassisted delivery, 2) assisted easy calving 3) assisted difficult calving 4) caesarean section and 5) foetotomy. As the incidence of foetotomy was less than 0.5%, the last two ordinal categories were combined, leaving a total of four mutually exclusive categories. The general frequencies of first parity calving ease scores in the data set were 951 (10.75%) for unassisted delivery; 5,514 (62.32%) for assisted easy calving; 1,316 (14.88%) for assisted difficult calving; and 1,066 (12.05%) for caesarean section and foetotomy.

The effects of dam age, sex of the calf, and their interaction were considered by combining eight different age groups (20 to 23, 23 to 25, 25 to 27, 27 to 29, 29 to 31, 31 to 33, 33 to 35, and 35 to 38 months) with sex of calf for a total of 16 nominal subclasses. Herd-year-season (HYS) subclasses were created from combinations of herd, year, and two different seasons (from November to April and from May to October) as in Carnier *et al.* [7] who also analyzed calving ease data from this same population. The sire pedigree file was further pruned by striking out identifications of sires having no daughters with calving ease records and appearing only once as either a sire or a maternal grandsire of a sire having daughters with records in the data file. Pruning results in no loss of pedigree information on parameter estimation yet is effective in reducing the number of random effects and hence computing demands. The number of sires remaining in the pedigree file after pruning was 1,929. Therefore, as in Kizilkaya *et al.* [21], the CP and CT models used for the analysis of calving ease data included the fixed effects of age of dam classifications, sex of calf and their interaction in $\boldsymbol{\beta}$, the random effects of independent herd-year-season effects in **h**, random sire effects in **s** and random maternal grandsire effects in **m**. We assume:

$$\begin{pmatrix} \mathbf{s} \\ \mathbf{m} \end{pmatrix} \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{G} = \mathbf{G}_o \otimes \mathbf{A}\right)$$

and

$$\mathbf{h} \sim N\left(\mathbf{0}, \mathbf{I}\sigma_h^2\right)$$

where $\mathbf{G}_0 = \begin{pmatrix} \sigma_s^2 & \sigma_{sm} \\ \sigma_{sm} & \sigma_m^2 \end{pmatrix}$, with σ_s^2 denoting the sire variance, σ_m^2 denoting the maternal grandsire variance, σ_{sm} denoting the sire-maternal grandsire covariance, and σ_h^2 denoting the HYS variance. Furthermore, $\otimes$ denotes the Kronecker (direct) product (Searle [35]), and **A** is the numerator additive relationship matrix between sires due to identified male ancestors (Henderson [18]). Also, **h** is assumed independent of **s** and **m.** Flat unbounded priors were placed on all fixed effects and variance components. Based on preliminary analyses of the data and results from the simulation study, v was not inferred upon but held constant to $v = 4$ in the CT model. MCMC inference was based on the running of three different chains for each model. For each chain in the CP model, a total of 5,000 cycles of burn-in period followed by saving samples from each of 100,000 additional cycles was executed based on the experiences of Kizilkaya *et al.* [21]. Because of initially anticipated slower mixing, the corresponding burn-in period for each chain in the CT model was 10,000 cycles followed by saving each of 200,000 additional cycles. To facilitate diagnosis of MCMC convergence by 5,000 cycles, the starting values on variance components for each chain within a model were widely discrepant, with one chain starting at the posterior mean of all (co)variance components based on a preliminary analysis, another chain starting at the posterior mean minus 3 posterior standard deviations for each (co)variance component and the final chain starting at the posterior mean plus 3 posterior standard deviations for each (co) variance component.

For both the simulation study and the calving ease data analysis, the effective number of independent samples (ESS) for each parameter was determined using the initial positive sequence estimator of Geyer [16] as adapted by Sorensen *et al.* [36]. Furthermore, key genetic parameters, specifically direct heritability (h_d^2), maternal heritability (h_m^2) and the direct-maternal genetic correlation (r_{dm}) were inferred upon in the calving ease data using the functions of $\mathbf{G}_0$ as presented by Kizilkaya *et al.* [21] and Luo *et al.* [23], for example. The only difference in the computation of heritabilities between the CP and the CT model was that the marginal residual variance for the underlying liabilities is not σ_e^2 in CT, as it is in CP, but is equal to $\frac{v}{v-2}\sigma_e^2$ (Stranden and Gianola [39]). Posterior means and standard deviation of elements of $\mathbf{s}$ were also compared between the CP and the CT model.

RESULTS

Simulation Study

Table I summarizes inference on v based on the replicated datasets from the two populations, comparing the CP versus CT models for the analysis of ordinal categorical data and comparing the Gaussian linear mixed model versus the *t*-error linear mixed model for the analysis of the matched latent or underlying normal liabilities, as if they were directly observed. The inference on v was surprisingly sharp and seemingly unbiased for the *t*-error mixed model analysis of liability data from Population I (v=4), with 95% equal-tailed posterior probability intervals (PPI) not exceeding 1.5 in width; furthermore, the corresponding ESS were relatively large indicating stable MCMC inference. Conversely, inference on v based on the *t*-error mixed model analysis of liability data from Population II ($v = \infty$) indicated extremely wide 95% PPI and posterior means exceeding 100, correctly indicating stronger evidence of Gaussian distributed versus *t*-distributed residuals for data from that population. Furthermore, ESS were generally very small (~ 20) indicating that inference on v was rather unreliable for data from Population II, at least given the specified MCMC sampling scheme. That is, five times as many MCMC samples would be needed to attain a minimum ESS of 100 as advocated by previous investigators ([5, 41]).

Inference on v in ordinal data under the CT model was also interesting. In Population I, the 95% PPI correctly concentrated on low values for v although the PPI were understandably wider than for the corresponding analyses of liability data under *t*-error linear mixed models. Also, the ESS on v were considerably smaller (<25) for the CT model analysis of ordinal data than for the corresponding matched linear model analyses of liability data, such that acceptably accurate inference on v would require substantially more sampling. In replicated ordinal data from Population II, the 95% PPI on v were wide and concentrated on high values of v, consistent with what was expected. Furthermore, as with the *t*-error mixed model analysis of liability data, MCMC mixing on v using the CT model on ordinal data was seen to be particularly problematic in Population II as manifested by the small ESS.

Table II summarizes inference on σ_s^2 based on the replicated datasets from the two populations, comparing the CP versus CT models for the analysis of ordinal categorical data and comparing the Gaussian linear mixed model versus the *t*-error linear mixed model for the analysis of the underlying liabilities. In the analyses of liability data from replicated datasets from both populations, the 95% PPI were in good agreement with σ_s^2=0.10; furthermore, very large ESS indicating very good MCMC mixing.

MCMC mixing on σ_s^2 was understandably slower in the analysis of ordinal categorical data, particularly in replicated data from Population II using CT due to the generally high posterior sampling correlation between σ_s^2 and v.

Because of the problem of MCMC mixing of v in ordinal data, the MCMC chains were rerun with v held constant ($v = 4$) for the DIC and LML comparisons between models. In Table III, the DIC and the LML are given for each replicated dataset within each population for the CP versus the CT model analyses of ordinal data and for the Gaussian linear mixed model versus the *t*-error linear mixed model analyses of liability data. Speigelhalter *et al.* [37] suggested that a DIC difference exceeding 7 to be a substantial indication of an important difference in model fit. Given that, the model choices based on DIC for the linear mixed model analyses of liability data were resoundingly in favor of the correct model. However, in the comparison between CP and CT models for ordinal data analysis, the correct (CT) model was decisively chosen in only one of the replicates of Population I ($v = 4$) whereas the correct (CP) model was decisively chosen in only two of the replicates of Population II ($v = \infty$), the other comparisons being somewhat indecisive (i.e. DIC differences < 7). This may not be too surprising given the information content of ordinal data relative to underlying continuous liability data. Comparisons based on LML (larger is better) lead to similar conclusions as those based on DIC (smaller is better).

Application to Calving Ease Scores in Italian Piemontese Cattle

Genetic Parameter Inference

Sire and maternal grandsire CP and CT models were used for the analysis of calving ease scores in Italian Piemontese cattle. Because of the MCMC mixing problems encountered in inferring upon v, this parameter was held constant to $v = 4$. Posterior inferences on key genetic parameters are summarized in Table IV and are based on the combined results from each of the three separate chains. The posterior mean, median and modal estimates (not shown) of the two heritabilities, and the genetic correlation using the MCMC algorithms were similar to each other within both models, implying that the posterior densities were symmetric and unimodal; this was further manifested by the fact that the 95% PPI are closely matched by the posterior mean ± 2 standard deviations. In this study the total ESS for dispersion parameters across the three chains ranged from 1,420 to 9,305, indicating sufficient MCMC mixing under both models. Table IV shows that the ESS from the CT model were found to be almost double those of the CP model, attributable to the twice as large post-burn-in period for CT model. Considering v as known also improves mixing of, particularly, genetic parameters, in the CT model relative to joint inference with v (results not shown). Although the n x 1 auxiliary variable vector $\boldsymbol{\lambda}$ is included in the CT model, this augmentation does not appear to adversely impact ESS and hence mixing of key genetic parameters relative to the CP model.

In this study, the CT model produced posterior means of genetic variance components that were nearly twice as large as those estimated using the CP model. Furthermore, the marginal residual variance is $\frac{v}{v-2}\sigma_e^2$ in the CT model such that seemingly twice as much residual variance is inferred under a CT model (with $v = 4$) than under a CP model (with $\nu = \infty$). Although these results might at first sight imply that greater genetic and residual variation is directly captured by the CT model, it should be realized that the variance of underlying variables **L** is only defined proportionately to the marginal residual variance. This is further apparent in that the 95% PPI of heritabilities were only very slightly concentrated towards lower values in the CT model relative to the CP model such that the corresponding 95% PPI for both h_d^2 and h_m^2 overlapped substantially between the two models. Furthermore, the posterior density of r_{dm} was very similar between CT and CP, with most of the density being between -0.2 and -0.8.

In order to compare the CP and CT models for fit to the calving ease data, LML and DIC values, broken down into its components $\bar{D}$ and p_D, are reported in Table V. Since it is difficult to quantify the degree of Monte Carlo error on DIC (Zhu and Carlin [47]), we report DIC and LML values separately for each of the three chains under each model. It can be seen that there are relatively inconsequential differences in the measures from one chain to the next within each model relative to between models, thereby indicating considerably small Monte Carlo errors on the DIC difference between the two models. Both model choice criteria were overwhelmingly in favor of the CT model with $\nu = 4$. As anticipated, the model complexity, as measured by p_D, is higher for the CT model; however, the complexity penalty is strongly counteracted by a smaller mean deviance $\bar{D}$, thereby resulting in a smaller DIC favoring choice of the CT model.

Inferences on Sire Effects

Posterior means of elements of $\mathbf{s}$ were determined to be corresponding point estimates of progeny differences (EPD) under both CT and CP models. The relationships between these estimates are shown to be strongly linear in Figure 1, with no hint of substantial reranking as indicated by a Pearson correlation of 0.99. The CT model had greater spread in EPD's compared to the CP model, as further manifested by a least-squares estimated slope of 1.38. This is not too surprising since a larger additive genetic (sire) variance was inferred in the CT model such that posterior means of elements of $\mathbf{s}$ should be more dispersed in the CT model relative to the CP model. However, as discussed later, this is not practically important since the variance of $\mathbf{L}$ is defined only proportionately to the marginal residual variability which is also larger in the CT model.

Posterior standard deviations of elements of $\mathbf{s}$ are analogous to standard errors of prediction in mixed effects model analysis and can be used to derive approximate reliabilities of EPD's (Wang *et al.* [46]). That is, the standard errors of prediction were simply determined as the standard deviation of the MCMC samples of elements of $\mathbf{s}$. Figure 2 provides scatter plots of these standard errors with the corresponding least squares regression line for the CT model versus the CP model. In this case, the correlation between the estimated standard errors was near unity. The estimated slope was nearly 1.41 indicating that the posterior standard errors were on average 41% larger under the CT model than under the CP model; nevertheless, these need to be considered proportionately to σ_s^2 which was also larger under the CT model.

DISCUSSION

Given the recent momentum in using heavy-tailed residual specifications for the analysis of production data in animal breeding ([32, 38, 39, 44]) a hierarchical threshold (CT) mixed model based on a cumulative *t*-link specification was developed, validated by simulation and applied to a small calving ease dataset from Italian Piemontese cattle. The simulation study indicated that inference on ν is possible in a CT model; however, it appears that either a more suitable MCMC strategy is needed or many more samples are required than pursued in our study to ensure a more reliable inference on ν. Until this issue is satisfactorily resolved, we advocate fixing ν at some arbitrarily low value in a CT model analysis. We chose $\nu = 4$ since this value minimally assures defined first, second, and third moments while providing a liability variable distribution that is maximally heavy-tailed. One can then use model choice criteria such as DIC to assess whether or not the CT model is a better data fit than the CP model. We further note that for the case where ν is fixed, that MCMC mixing was not negatively affected by using the CT model, even though our data augmentation (of $\boldsymbol{\lambda}$) implementation might be of concern to those who might prefer Metropolis-Hastings sampling on all parameters (von Rohr and Hoeschele [44]) instead of introducing augmented variables. More recently, it has been demonstrated that data augmentation can be strategically used to enhance MCMC mixing; the strategies discussed by van Dyk and Meng [42] may facilitate more favorable mixing on ν and hence deserve further consideration in CT model applications to animal breeding. Of particular note was that due to the implementation of the algorithm of Cowles[11], MCMC mixing of $\boldsymbol{\tau}$ was not seen to have been the most limiting (results not reported) as in previous animal breeding implementations ([36],[43]).

Our point estimates for heritabilities are substantially higher than corresponding threshold model estimates for calving ease reported by Manfredi *et al.* [25, 26], McGuirk *et al.* [28, 29], Varona *et al.* [43], Luo *et al.* [23], and Bennett and Gregory [2]. Nevertheless, our inference on a strongly negative direct-maternal genetic correlation is in agreement with previous work on calving ease using threshold models ([2, 23, 43]) and linear mixed models using data from the same source (Carnier *et al.* [7]). Hence, it appears from our results, in agreement with other studies, that selection of sires for calving ease of their progeny as calves should result in antagonistic effects in the ability of their daughters to calve easily as dams in successive generations. What was most surprising is that the 95% PPI for h^2_d are greater and do not overlap with corresponding PPI in Kizilkaya et al. (2002) who used a larger data set on first parity records from herds with greater than 50 rather than 100 records over the nine year period from the same data source. This result may be indicative of heterogeneity in genetic and residual variance due to size of herd or other confounding factors (e.g. region); this is an area for further research that our group has started with respect to residual variability.

Two Bayesian model choice criteria, DIC and LML, were used to choose between the CP and CT models. In a simulation study, it was demonstrated that both DIC and LML were able to decisively choose the correct model in most cases whereas, in the remaining cases, these measures were too similar between the two models to allow a definitive choice. In the analysis of calving ease scores in Italian Piemontese cattle, the CT model was overwhelmingly chosen as the best fitting model by both model choice criteria. Nevertheless, in the examination of EPD's there were no real tangible differences between the two models in terms of sire genetic rankings. Although the posterior standard deviations of sire progeny merit appear to be greater in the CT model relative to the CP model, the impact on reported accuracies of these predictions would be shown to be negligible. For example, the Beef Improvement Federation (USA) measure (Wang *et al.* [46]) of accuracy is somewhat directly related to the genetic variance which is higher in the CT versus the CP model.

Our study involved sire models, where calf records are connected directly to sires with genetic relationships identified only through known paternal ancestry. Sire models are different from animal models where each record is connected directly to a calf identification with all known genetic (maternal and paternal) relationships explicitly modeled. For animals (e.g. dams), with effectively less data information, we would anticipate greater differences in predicted genetic merit between CT and CP animal models than given in our study. However, a sire model has been seen to be more stable than an animal model in CP implementations (Mayer [27]), particularly when paternal half-sib relationships are predominant as in our data. Furthermore, the fact that a sire and maternal grandsire model only accounts directly for a portion of the additive genetic variance and of the maternal genetic variance implies that a *t*-error assumption is essentially placed on a composite source of error, i.e. the sum of the residual variance and remaining genetic variation, attributable to unknown dams and to Mendelian sampling. From the perspective of using heavy tailed densities to mute residual outliers, this is significant since deviant dam and/or Mendelian sampling effects may be muted as well in a CT sire model specification.

Presently, it does not appear to be feasible to apply MCMC methods to the very large datasets used for routine genetic evaluation of livestock by breed associations and national recording organizations. Kizilkaya *et al.* [21] recently demonstrated, however, very little differences in predicted genetic merit and standard error of prediction in a CP sire model between inference provided by MCMC and by approximate empirical Bayes procedures currently utilized by the industry (e.g. Berger [3]). Empirical Bayes procedures are based on using the joint posterior modes of the sire effects as the EPD's, conditional on estimated variance components as if they were known with certainty. Based on results from Gianola and Foulley [17], the CT model can be readily implemented using empirical Bayes methods since the probability density function and the cumulative density function of a standard Student t distribution could be substituted for the corresponding Gaussian functions needed to derive the necessary scoring equations used to determine the required joint posterior modes. Furthermore, the degrees of freedom parameter, v, could be jointly estimated with the variance components using Laplace's method and tested for statistical significance using marginal likelihood ratio tests (Tempelman and Gianola [40]). Empirical Bayes implementation of the CT sire model and the comparison of results with MCMC inference under the CT sire model deserve further consideration. Unfortunately, however, these comparisons may not necessarily apply to CP or CT animal models since joint modal estimates of EPD's in the CP animal model can be badly biased (Mayer [27]).

In this study, we have considered only two cumulative link models for the analysis of calving ease; conceptually, there are many others including those proposed by Chen and Dey [8]. In fact, Albert and Chib [1] demonstrate that the cumulative logistic link model is roughly equivalent to the CT model with $v = 8$. Other models can be contrived by considering alternative heavy-tailed distributions for the underlying variables, such as those considered by Rosa [32]. Some of the resulting models may be shown to have better fit to calving ease data than demonstrated with the CT model in our paper. Specifications based on skewness (Von Rohr and Hoeschele [44]) may also have merit.

The substantial residual and genetic correlations between birth weight and calving difficulty imply that genetic evaluations of calving ease would substantially benefit from a bivariate threshold/linear multiple trait analysis with birth weight ([24, 43]). Further work on providing modeling flexibility with *t*-distributed specifications on both traits jointly is needed given our results and those already presented by Stranden and Gianola [38, 39] and Rosa [32].

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Table I. Posterior inference on the residual degrees of freedom parameter (ν) in simulation study using the cumulative *t*-link model.

	Liability Data			Ordinal data		
Population-Dataset[a]	PM ± SD[b]	95% PPI[c]	ESS[d]	PM ± SD[b]	95% PPI[c]	ESS[d]
I-1	3.70 ± 0.30	3.15 - 4.31	1,849	5.58 ± 1.79	3.58 - 10.36	74
I-2	4.22 ± 0.35	3.59 - 4.97	1,927	7.28 ± 3.02	4.01 - 15.20	86
I-3	4.26 ± 0.36	3.61 - 5.03	1,781	9.57 ± 15.85	3.84 - 35.38	38
II-1	276 ± 373.21	42.53 - 1328.10	21	20.13 ± 38.93	4.08 - 126.20	20
II-2	144 ± 176.50	21.99 - 653.56	20	121.05 ± 209.46	6.04 - 862.12	17
II-3	324 ± 444.38	30.69 - 1576.98	13	39.75 ± 97.82	4.20 - 411.63	16

[a] Population I specified with *t* residual distribution with 4 degrees of freedom; Population II specified with Gaussian residual distribution. Each population replicated for 3 datasets each.

[b] Posterior mean ± standard deviation.

[c] 95% equal-tailed posterior probability interval.

[d] The effective number of independent samples using the initial positive sequence estimator of Geyer (1992).

Table II. Posterior inference on sire variance (σ_s^2) in simulation study using the cumulative *t*-link model.

	Liability Data			Ordinal data		
Population-Dataset[a]	PM ± SD[b]	95% PPI[c]	ESS[d]	PM ± SD[b]	95% PPI[c]	ESS[d]
I-1	0.13 ± 0.03	0.08 - 0.21	39,722	0.11 ± 0.03	0.06 - 0.19	2,998
I-2	0.14 ± 004	0.08 - 0.22	41,817	0.13 ± 0.04	0.08 - 0.22	1,775
I-3	0.10 ± 0.03	0.05 - 0.16	31,969	0.08 ± 0.03	0.04 - 0.14	966
II-1	0.10 ± 0.03	0.06 - 0.15	46,915	0.11 ± 0.03	0.06 - 0.19	185
II-2	0.12 ± 0.03	0.07 - 0.18	47,911	0.13 ± 0.04	0.08 - 0.22	130
II-3	0.08 ± 0.02	0.05 - 0.13	42,514	0.12 ± 0.03	0.07 - 0.19	187

[a] Population I specified with *t* residual distribution with 4 degrees of freedom; Population II specified with Gaussian residual distribution. Each population replicated for 3 datasets.

[b] Posterior mean ± standard deviation.

[c] 95% equal-tailed posterior probability interval.

[d] The effective number of independent samples using the initial positive sequence estimator of Geyer (1992).

Table III. Deviance information criteria (DIC) and log marginal likelihood (LML) comparisons between models in simulation study.

	Analysis of liability data				Analysis of categorical data			
	Gaussian error model		Student t_4-error model		Cumulative probit link model		Cumulative t_4-link model	
Population-Dataset[a]	DIC	LML	DIC	LML	DIC	LML	DIC	LML
I-1	8,782	-4,392	8,426	-4,213	5,596	-2,798	5,587	-2,794
I-2	8,711	-4,356	8,344	-4,172	5,734	-2,867	5,735	-2,868
I-3	8,816	-4,409	8,492	-4,246	5,727	-2,864	5,726	-2,863
II-1	7,131	-3,566	7,246	-3,625	5,322	-2,661	5,325	-2,663
II-2	7,180	-3,590	7,287	-3,646	5,172	-2,586	5,184	-2,592
II-3	7,237	-3,618	7,358	-3,682	5,443	-2,722	5,447	-2,723

[a] Population I specified with *t* residual distribution with 4 degrees of freedom; Population II specified with Gaussian residual distribution. Each population replicated for 3 datasets.

Table IV. Posterior inference on genetic parameters of calving ease scores in Italian Piemontese cattle.

	Cumulative probit link model			Cumulative t-link model		
Parameter[a]	PM ± SD[b]	95% PPI[c]	ESS[d]	PM ± SD[b]	95% PPI[c]	ESS[d]
σ_s^2	0.146 ± 0.026	0.101 - 0.200	3,281 [925 - 1,261]	0.274 ± 0.047	0.189 - 0.373	5,517 [1,745 – 1,984]
σ_m^2	0.039 ± 0.011	0.019 - 0.063	1,346 [336 - 569]	0.060 ± 0.019	0.027 - 0.100	2,022 [573 – 845]
σ_{sm}	0.027 ± 0.013	0.002 - 0.053	1,791 [557 – 655]	0.054 ± 0.023	0.010 - 0.099	2,871 [897 – 1,068]
σ_h^2	0.153 ± 0.019	0.118 – 0.192	9,305 [2,899 – 3,232]	0.308 ± 0.036	0.241 – 0.382	12,264 [3,666 – 4,503]
H^2_d	0.42 ± 0.07	0.30 - 0.56	2,873 [833 – 1,086]	0.40 ± 0.06	0.28 - 0.53	4,827 [1,486 – 1,786]
H^2_m	0.14 ± 0.04	0.07 - 0.23	1,461 [461 – 506]	0.11 ± 0.04	0.05 - 0.19	2,309 [748 – 801]
r_{dm}	-0.55 ± 0.14	-0.78 - -0.23	1,420 [456 - 498]	-0.58 ± 0.15	-0.82 - -0.24	2,135 [620 – 877]

[a] See text for description.

[b] Posterior mean ± standard deviation.

[c] 95% equal-tailed posterior probability interval.

[d] The total effective number of independent samples across the three MCMC chains using the initial positive sequence estimator of Geyer (1992).; interval values [ ] refer to range in ESS across the three chains.

Table V. MCMC chain-specific deviance information criterion (DIC) and log marginal likelihood (LML) values for the analysis of calving ease scores in Italian Piemontese cattle.

	$\bar{D}^{a}$	$D(\theta)^{b}$	$P_D{}^{c}$	*DIC*	LML
Cumulative Probit					
Chain 1	16,564	15,782	782	17,346	-8,705
Chain 2	16,562	15,780	782	17,344	-8,705
Chain 3	16,562	15,779	783	17,345	-8,705
Cumulative t-link					
Chain 1	16,348	15,525	823	17,172	-8,634
Chain 2	16,346	15,521	825	17,171	-8,634
Chain 3	16,348	15,524	824	17,172	-8,634

[a] The average of Bayesian deviance.

[b] Bayesian deviance based on posterior mean vector.

[c] The effective number of parameters.

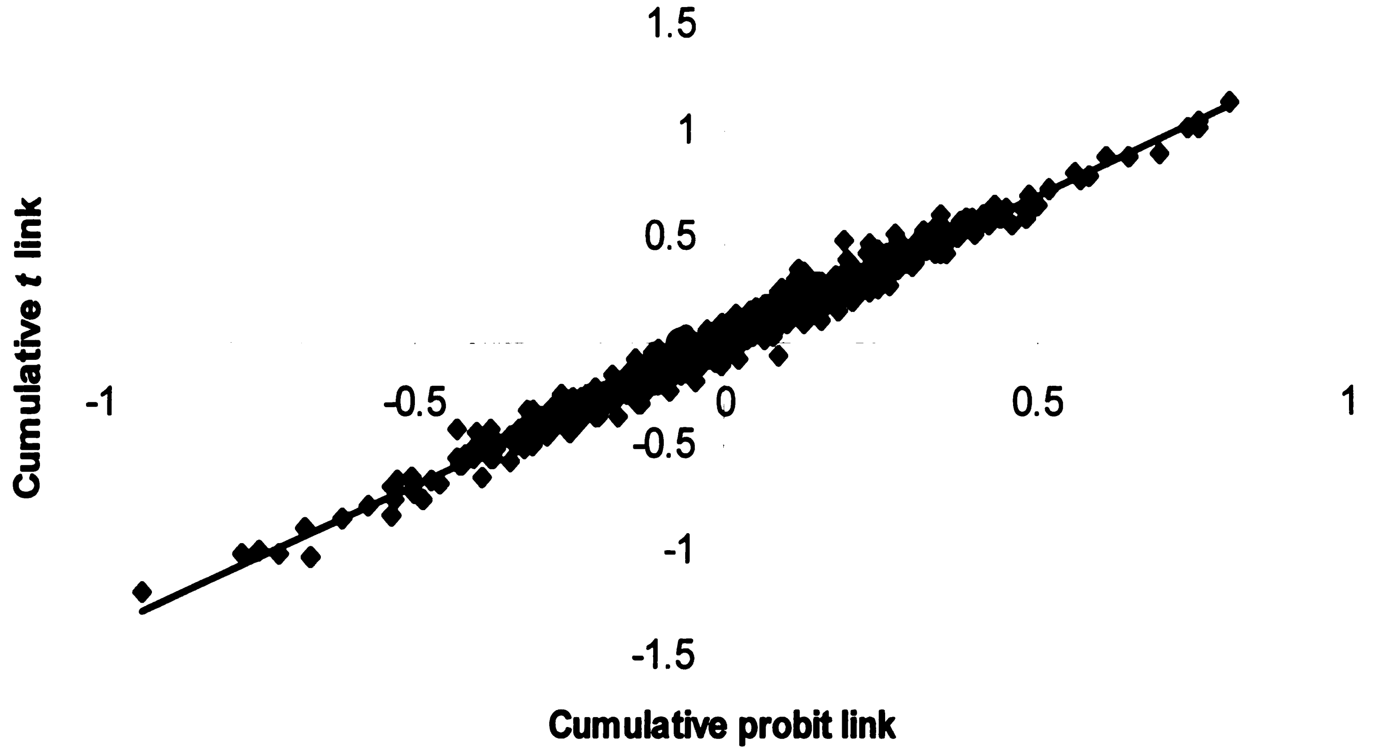

Figure 1. Scatterplot of posterior means of estimated sire progeny differences based on cumulative *t*-link versus cumulative probit link model with superimposed line of best fit.

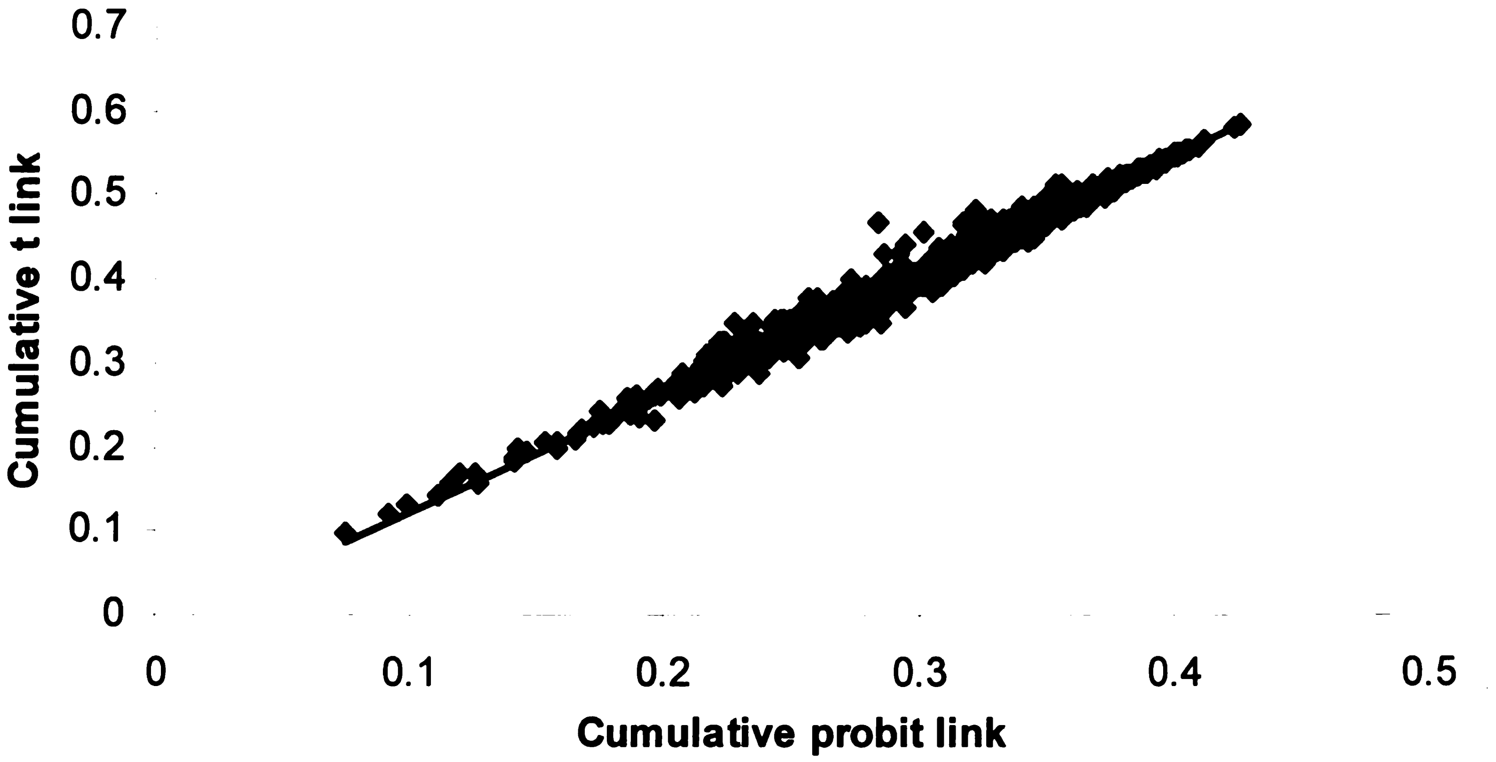

Figure 2. Scatterplot of posterior standard deviations of estimated sire progeny differences based on cumulative *t*-link versus cumulative probit link model with superimposed line of best fit.

CHAPTER 4

Bayesian structural modeling of heterogeneous residual variances in generalized linear mixed models

ABSTRACT

A Bayesian hierarchical generalized linear mixed model (GLMM) based on a structural multifactorial model with fixed and random effects that multiplicatively influence residual heteroskedasticity was developed. The two specific GLMM considered in this paper are the linear mixed model (LMM) for the analysis of normally distributed characters like birth weight and the threshold or cumulative probit mixed model (CPMM) for the analysis of ordinal categorical data like calving ease. We validated our models using Markov Chain Monte Carlo (MCMC) methods for posterior inference on parameters specifying residual heteroskedasticity. Three replicated datasets on normally distributed and ordinal categorical data from each of four different populations, characterized by various levels of residual heteroskedasticity, were generated. Residual heteroskedasticity parameters, including fixed and random effects specifications, were particularly well estimated for the analysis of normal data and when heteroskedasticity was extreme. Furthermore, the deviance information criterion (DIC) was useful in correctly choosing between heteroskedastic and homoskedastic models. Sire and maternal grandsire heteroskedastic linear and cumulative probit link threshold models were fitted, respectively, to birth weight (BW) and calving ease (CE) data on 8,847 Italian Piemontese first parity dams. The residual variance for male calves was significantly greater than that for female calves for both BW and CE, translating to substantial differences in the posterior means ± standard deviations of direct heritabilities

for BW (0.32 ± 0.05 for females versus 0.25 ± 0.04 for males) and for CE (0.504 ± 0.083 for females versus 0.370 ± 0.064 for males). Although the heteroskedastic LMM and CPMM were chosen by DIC as the better fitting model for BW and CE, respectively, the high correlation between posterior means of sire effects (>0.97) suggested no meaningful rerankings.

INTRODUCTION

An important assumption in many genetic evaluation models is that variance components associated with random and residual effects are homogeneous across all conditions, whether it be across sexes of animal or environmental conditions, such as herds. These models are said to be homoskedastic. However, the existence of heterogeneous variances, or heteroskedasticity, for milk production ([16], [18]), growth performance (Garrick *et al.* [9]) and conformation traits (Robert-Granie *et al.* [30]) has been firmly established.

A number of possible causes for heteroskedasticity have been suggested, including a positive relationship between herd means and variances, differences across geographical regions, and changes in variability over time due to changing herd managements (Weigel *et al.* [40]). If this phenomenon is not properly taken into account in generalized linear mixed models, differences in within-subclass variances can result in biased breeding value predictions with disproportionate numbers of animals selected from environmental subclasses characterized by high variability. This bias potentially translates into a reduced genetic progress due to breedstock selection based on these predictions ([17], [40]).

Generalized linear mixed models (GLMM) can be readily extended to take into account heteroskedasticity. As an example, best linear unbiased prediction (BLUP) can be reliably used in breedstock selection when random effects and residual variances are heterogeneous, provided they are correctly specified across subclasses characterized by unique variance components (Gianola [12]). However, variance components are rarely known and may need to be estimated for a large number of small subclasses when heteroskedasticity is present. Since most preferred methods of variance components estimation, including maximum likelihood (ML) and restricted maximum likelihood (REML), have only asymptotically desirable properties, such procedures may not yield reliable estimates within small subclasses ([40], [41]).

Foulley *et al.* [7] introduced an empirical Bayes procedure for assessing sources of residual heteroskedasticity in Gaussian linear mixed models (LMM). Their method was based on the use of a structural log link model $\gamma_i = \ln\sigma^2_{e_i} = \mathbf{m}'_i\boldsymbol{\lambda}$, where $\sigma^2_{e_i}$ is the residual variance component specific to subclass *i*, $\mathbf{m}_i$ is a known incidence matrix unique to subclass *i* connecting $\sigma^2_{e_i}$ to $\boldsymbol{\lambda}$, a vector of unknown dispersion parameters. Hypothesis testing on elements of $\boldsymbol{\lambda}$ was based on an approximate marginal likelihood ratio test. In addition, Foulley *et al.* [7] and San Cristobal *et al.* [32] further extended the structural log link model such that $\boldsymbol{\lambda}$ includes both "fixed" and "random" factor partitions. As in a classical linear model, the distinction between these two classes of effects for modeling heteroskedasticity is such that levels of a random factor derive from a probability distribution (Searle *et al.* [33]); that is, a structural prior is placed on random effects. Conversely, fixed effects involve parameters that might be characterized by subjective or noninformative priors. For example, sex of animal might be considered fixed whereas herds might be considered random with respect to a structural classification model for heteroskedasticity (San Cristobal *et al.* [32]). As with random location effects in classical linear mixed effects models, specifying structural priors on effects influencing heteroskedasticity is particularly beneficial in that statistical information on one effect (e.g. herd) is borrowed from the distribution of all such effects within the same factor (Robinson [31]).

Foulley and Gianola [8] adapted the structural log linear fixed effects model for heterogeneous residual variances in a threshold or cumulative probit mixed model (CPMM), using likelihood procedures for residual heteroskedastic inference on calving ease in American Simmentals as a function of sex of calf and age of dam. Ducrocq [6] analyzed calving ease data of French dairy breeds (Normande and Montbeliarde) using the methods developed by Foulley and Gianola [8] method, considering the effects of sex, age of dam, parity, region, and year on residual heteroskedasticity on calving ease scores.

Many of the proposed residual heteroskedastic models for animal breeding, however, invoke analytical approximations, which appear tenuous, particularly for the analysis of categorical data. Furthermore, we perceive the lack of a unifying framework for structural modeling of heterogeneous variances in GLMM analysis for both continuous production and categorical fitness traits. That is, structural prior or random effects specifications have been developed for Gaussian error models, as by Foulley *et al.* [7] and San Cristobal *et al.* [32] but not for any other GLMM, such as the CPMM, in animal breeding. The objectives of our study were 1) to develop and validate a Bayesian structural multiplicative model on residual variances for observed or augmented variables in a heteroskedastic GLMM, concentrating on a LMM analysis of normal data and a CPMM analysis of ordinal data based on use of Markov Chain Monte Carlo (MCMC) methods and 2) to apply the model using MCMC to a calving ease dataset derived from the Italian Piemontese population.

MATERIALS and METHODS

HIERARCHICAL CONSTRUCTION OF THE HETEROSKEDASTIC GENERALIZED LINEAR MIXED MODEL

In a number of GLMM, data augmentation schemes exist such that a nx1 vector of either observed or augmented variables $\mathbf{L}=\{L_i\}_{i=1}^{n}$ conceptually maps one-to-one to the data vector $\mathbf{Y}=\{Y_i\}_{i=1}^{n}$. Examples where such augmented variables are useful include threshold models (Sorensen *et al.* [34]) and censored data models (Sorensen *et al.* [35]). We write a linear mixed effects model as

$$\mathbf{L}=\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{u}+\mathbf{e} \tag{1}$$

where $\boldsymbol{\beta}$ is a vector of fixed location effects, **u** is a vector of random location effects, **X** and **Z** are known design matrices and **e** is a vector of normally distributed residuals with variance covariance matrix **R** having a certain heteroskedasticity specification as defined later. The linear model in (1) is equivalent to the following distributional specification:

$$\mathbf{L}\mid\boldsymbol{\beta},\mathbf{u},\mathbf{R}\sim p(\mathbf{L}\mid\boldsymbol{\beta},\mathbf{u},\mathbf{R})=N(\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{u},\mathbf{R}) \tag{2}$$

For normally distributed data as in a LMM, $\mathbf{y}\equiv\mathbf{L}$ such that $p(\mathbf{Y}\mid\boldsymbol{\beta},\mathbf{u})\equiv p(\mathbf{L}\mid\boldsymbol{\beta},\mathbf{u})$ whereas for ordinal data with, say, $C=4$ categories, **L** maps to **y** as follows:

$$Y_i = \begin{cases} 1 & \tau_o < L_i \le \tau_1 \\ 2 & \tau_1 < L_i \le \tau_2 \\ 3 & \tau_2 < L_i \le \tau_3 \\ 4 & \tau_3 < L_i < \tau_4 \qquad i = 1....n \end{cases} \tag{3}$$

where $\tau_0 = -\infty < \tau_1 < \tau_2 < \tau_3 < \tau_4 = \infty$ are threshold parameters that define bin boundaries for **y** based on **L**.

We further partition e according to residual variance subclasses $\mathbf{e}' = \begin{bmatrix}\mathbf{e}'_{11} & \mathbf{e}'_{12} & \cdots & \mathbf{e}'_{st}\end{bmatrix}$ where $\mathbf{e}_{kl} \sim N\left(\mathbf{0}, \mathbf{R}_{kl} = \mathbf{I}_{n_{kl}}\sigma^2_{e_{kl}}\right)$ pertains to the n_{kl}x1 subvector of residuals identified with the k^{th} level (k=1,2,....s) of a fixed effect subclass (e.g. sex) and l^{th} level (l=1,2,....t) of a random effect subclass (e.g. herd) that jointly influence the residual variance for the kl^{th} subclass. For pedagogical purposes, we just concentrate on the effect of one fixed factor and one random factor on residual heteroskedasticity but extensions to additional factors are possible. We partition the data $\mathbf{y}' = \begin{bmatrix}\mathbf{y}'_{11} & \mathbf{y}'_{12} & \cdots & \mathbf{y}'_{st}\end{bmatrix}$ and the corresponding augmented variables $\mathbf{L}' = \begin{bmatrix}\mathbf{L}'_{11} & \mathbf{L}'_{12} & \cdots & \mathbf{L}'_{st}\end{bmatrix}$ accordingly. We propose a multiplicative structural effects model as follows:

$$\sigma^2_{e_{kl}} = \bar{\sigma}^2_{e_k}\delta_l, \quad k=1,2,...s;\ l=1,2,....t. \tag{4}$$

where $\bar{\sigma}^2_{e_k}$ is the residual variance identified with the k^{th} level of the fixed effect subclass and $\delta_l > 0$ is a random multiplicative scaling factor unique to the l^{th} level of the random effect. Note then that fixed and random effects specifications are provided on both location and residual dispersion parameters, although the classes of effects considered do not need to be the same as for the log structural heteroskedastic models of Foulley *et al.* [7] and San Cristobal *et al.* [32].

The prior density on the fixed location effects $\boldsymbol{\beta}$ is specified

$$\boldsymbol{\beta} \sim p(\boldsymbol{\beta}) \tag{5}$$

where $p(\boldsymbol{\beta})$ is a subjective prior, typically specified to be flat or vaguely informative. Furthermore, the random location effects are typically characterized by a structural multivariate prior specification:

$$\mathbf{u}|\boldsymbol{\varphi} \sim p(\mathbf{u}|\boldsymbol{\varphi}) = N\left(\mathbf{0}, \mathbf{G}(\boldsymbol{\varphi})\right) \tag{6}$$

Here $\mathbf{G}(\boldsymbol{\varphi})$ is a variance-covariance matrix that is a function of several unknown variance components or variance-covariance matrices in $\boldsymbol{\varphi}$, depending on whether or not there are multiple sets of random effects and/or specified covariances between these sets; an example of the latter is the covariance between additive and maternal genetic effects. Furthermore, flat priors, inverted Gamma densities, inverted Wishart densities or products thereof may be specified for the prior density on $\boldsymbol{\varphi}$,

$$\boldsymbol{\varphi} \sim p(\boldsymbol{\varphi}) \tag{7}$$

depending, again, on the number of sets of random effects and whether there are any covariances thereof (Jensen *et al.* [20]).

A subjective conjugate inverted-gamma prior density or, alternatively, a flat prior density may be specified separately for each $\bar{\sigma}^2_{e_k}$, i.e.

$$\bar{\sigma}^2_{e_k} \sim p\left(\bar{\sigma}^2_{e_k}\right) \tag{8}$$

for k =1,2,...,s. Conversely, a structural prior is used to model the random residual dispersion effects, δ_l, l= 1,2,...,t. We conveniently choose this structural prior to be an inverted-gamma density with parameters α_e and α_e-1,

$$p(\delta_l \mid \alpha_e) \propto \frac{(\alpha_e - 1)^{\alpha_e}}{\Gamma(\alpha_e)} (\delta_l)^{-(\alpha_e - 1)} \exp\left(-\frac{\alpha_e - 1}{\delta_l} \right); \qquad l = 1, 2, \ldots, t. \tag{9}$$

Here $E(\delta_1) = 1$ and $\mathrm{Var}(\delta_1) = \frac{1}{\alpha_e - 2}$ such that as $\alpha_e \to \infty$, the random dispersion effects influence on residual heteroskedasticity diminishes. Note that with the specification in (5), there is a borrowing of information across levels $l = 1, 2, \ldots, t$ of the random factor, just as there is for classical random effects modeling of location parameters. Generally, α_e is unknown such that a subjective prior may be placed on it. One noninformative prior used in our applications is specified as follows:

$$\alpha_e \sim p(\alpha_e) \propto \frac{1}{(1 + \alpha_e)^2} \tag{10}$$

which is identical to specifying a Uniform(0,1) prior on $\frac{1}{(1 + \alpha_e)}$.

The remaining hierarchical specifications in this heteroskedastic GLMM depend upon the first (data sampling) stage of the n x 1 data vector **y**. For a LMM analysis of normal error data, equation (1) would suffice (i.e. $\mathbf{y} \equiv \mathbf{L}$) such that no augmented variables are required, whereas for a CPMM analysis of ordinal data with C ordinal categories, numbered $j = 1,2,\ldots,C$, we would specify the first stage of our hierarchical model using Sorensen *et al.* [34]:

$$p(\mathbf{y} \mid \mathbf{L}, \boldsymbol{\tau}) = \prod_{i=1}^{n} \left\{ \sum_{j=1}^{C} 1\left(\tau_{j-1} < L_{ikl} < \tau_j\right) 1\left(y_{ikl} = j\right) \right\} \tag{11a}$$

followed by, using a scalar representation of (2),

$$L_{ikl} \mid \boldsymbol{\beta}, \mathbf{u}, \bar{\sigma}^2_{e_k} \delta_l \sim N\left(\mathbf{x}'_{ikl} \boldsymbol{\beta} + \mathbf{z}'_{ikl} \mathbf{u}, \bar{\sigma}^2_{e_k} \delta_l \right). \tag{11b}$$

Here L_{ikl} and y_{ikl} are the ith elements of L_{kl} and y_{kl}, respectively, whereas x'_{ikl} and z'_{ikl} are known incidence row vectors corresponding to subject i within the kl^{th} residual variance subclass for $k = 1,2\ldots,s$, $l = 1,2,\ldots,t$, and $i = 1,2,\ldots,n_{kl}$. As before, $\boldsymbol{\tau} = \begin{bmatrix}\tau_0 & \tau_1 & \cdots & \tau_C\end{bmatrix}'$ denotes a vector of unknown threshold parameters that delimit the augmented variables **L** into their respective observed data bins **y** with 1(.) denoting the indicator function having value 1 if the condition within the function is true, being 0 otherwise.

Recall previously that $\tau_0 = -\infty$ and $\tau_C = +\infty$ but further note that in addition τ_1 is fixed to an arbitrary constant in order to satisfy identifiability constraints as in Sorensen *et al.* [34]. We further adopt the alternative parameterization presented by Sorensen *et al.* [34] in which residual variance is explicitly modeled, rather than typically constrained to equal to 1, as typically invoked in homoskedastic error CPMM (Gianola and Foulley [13]). This specification thereby requires one additional constraint on $\boldsymbol{\tau}$, such that C-3 parameters in $\boldsymbol{\tau}$ are uniquely identifiable. A prior distribution on the uniquely identifiable elements of $\boldsymbol{\tau}$ may be specified provided that the order constraints on elements of $\boldsymbol{\tau}$ are satisfied (Sorenson *et al.* [34]), i.e.

$$\boldsymbol{\tau} = \begin{bmatrix}\tau_2 & \tau_3 & \cdots & \tau_{C-1}\end{bmatrix}' \sim p(\boldsymbol{\tau}); \qquad \tau_2 < \tau_3 < \cdots < \tau_{C-1} \tag{12}$$

Note that our parameterization of the heteroskedastic cumulative probit threshold model, as per Foulley and Gianola [8], does not readily extend to the modeling of binary outcomes since it is required that C-3 ≥ 0.

The joint posterior density of $\boldsymbol{\beta}, \mathbf{u}, \left\{\bar{\sigma}^2_{e_k}\right\}_{k=1}^{s}, \left\{\delta_l\right\}_{l=1}^{t}, \boldsymbol{\varphi}, \alpha_e$ and any other parameters necessary for the GLMM in question (i.e. **L** and $\boldsymbol{\tau}$ in the CPMM) is simply specified as the product of the various stages of the hierarchical model. That is, for the LMM where $\mathbf{y}=\mathbf{L}$, the joint posterior density of all unknowns specified to proportionality is:

$$
\begin{aligned}
&p\left(\boldsymbol{\beta},\mathbf{u},\left\{\sigma^2_{e_k}\right\}_{k=1}^{s},\left\{\delta_l\right\}_{l=1}^{t},\boldsymbol{\varphi},\alpha_e \mid \mathbf{y}\right)\\
&\propto p\left(\mathbf{y}\mid\boldsymbol{\beta},\mathbf{u},\left\{\sigma^2_{e_k}\right\}_{k=1}^{s},\left\{\delta_l\right\}_{l=1}^{t}\right)p(\boldsymbol{\beta})p(\mathbf{u}\mid\boldsymbol{\varphi})p(\boldsymbol{\varphi}) \qquad (13)\\
&\left(\prod_{k=1}^{s}p\left(\sigma^2_{e_k}\right)\right)\left(\prod_{l=1}^{t}p(\delta_l\mid\alpha_e)\right)p(\alpha_e)
\end{aligned}
$$

whereas for the CPMM,

$$
\begin{aligned}
&p\left(\mathbf{L},\boldsymbol{\tau},\boldsymbol{\beta},\mathbf{u},\left\{\sigma^2_{e_k}\right\}_{k=1}^{s},\left\{\delta_l\right\}_{l=1}^{t},\boldsymbol{\varphi},\alpha_e \mid \mathbf{y}\right)\\
&\propto p(\mathbf{y}\mid\mathbf{L},\boldsymbol{\tau})\,p\left(\mathbf{L}\mid\boldsymbol{\beta},\mathbf{u},\left\{\sigma^2_{e_k}\right\}_{k=1}^{s},\left\{\delta_l\right\}_{l=1}^{t}\right) \qquad (14)\\
&p(\boldsymbol{\tau})p(\boldsymbol{\beta})p(\mathbf{u}\mid\boldsymbol{\varphi})p(\boldsymbol{\varphi})\left(\prod_{k=1}^{s}p\left(\sigma^2_{e_k}\right)\right)\left(\prod_{l=1}^{t}p(\delta_l\mid\alpha_e)\right)p(\alpha_e)
\end{aligned}
$$

Note that $p\left(\mathbf{L}\mid\boldsymbol{\beta},\mathbf{u},\left\{\sigma^2_{e_k}\right\}_{k=1}^{s},\left\{\delta_l\right\}_{l=1}^{t}\right)$ is equivalent to (2) given that **R** is a function of

$\left\{\sigma^2_{e_k}\right\}_{k=1}^{s}$ and $\left\{\delta_l\right\}_{l=1}^{t}$.

A MCMC inference strategy requires determination of and sampling from the full conditional distributions (FCD) of each parameter or groupings thereof. The FCD for fixed and random location effects, regardless of whether inference is based on the LMM or the CPMM, can be readily shown to be multivariate normal

$$
\boldsymbol{\beta},\mathbf{u}\mid\boldsymbol{\varphi},\bar{\sigma}^2_{e_1},\bar{\sigma}^2_{e_2},\ldots,\bar{\sigma}^2_{e_s},\delta_1,\delta_2,\ldots,\delta_t,\alpha_e,\mathbf{y},\mathbf{L}\sim N\left(\begin{bmatrix}\hat{\boldsymbol{\beta}}\\ \hat{\mathbf{u}}\end{bmatrix},\left(\begin{bmatrix}\mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}\\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}+(\mathbf{G}(\boldsymbol{\varphi}))^{-1}\end{bmatrix}^{-1}\right)\right)
$$

(15)

where $\begin{bmatrix}\hat{\boldsymbol{\beta}}\\ \hat{\mathbf{u}}\end{bmatrix} = \begin{bmatrix}\mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}\\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}+\left(\mathbf{G}(\boldsymbol{\varphi})\right)^{-1}\end{bmatrix}^{-1}\begin{bmatrix}\mathbf{X}'\mathbf{R}^{-1}\mathbf{L}\\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{L}\end{bmatrix}$ is the typical mixed model solutions to $\boldsymbol{\beta}$ and $\mathbf{u}$ based on current MCMC-sampled values of **R**, **L**, and $\boldsymbol{\varphi}$. Furthermore, $\mathbf{R}^{-1} = \bigoplus_{k=1,\, l=1}^{k=s,\, l=t} \mathbf{R}_{kl}^{-1}$, $\mathbf{X} = \left\{\mathbf{x}'_{ikl}\right\}$, and $\mathbf{Z} = \left\{\mathbf{z}'_{ikl}\right\}$. Univariate strategies for sampling from (15) are elucidated in Wang *et al.* [39].

Using results from Sorensen *et al.* [34], it is straightforward to generate from the FCD of individual elements of **L** and $\boldsymbol{\tau}$ under the CPMM. We prefer, however, the Metropolis-Hastings and method of composition joint update of **L** and $\boldsymbol{\tau}$ presented by Cowles [5]. She demonstrated and we have further noted in our previous applications (Kizilkaya *et al.* [21 22]) that the resulting MCMC mixing properties using this joint update are vastly superior to using separate Gibbs updates on individual elements of **L** and $\boldsymbol{\tau}$ as outlined by Sorensen *et al.* [34].

For either the CPMM or the LMM, it is straightforward to generate elements of $\boldsymbol{\varphi}$ from their FCD using results presented in previous work. If some partitions of $\boldsymbol{\varphi}$ form a variance-covariance matrix, then their respective FCD can be readily shown to be inverted-Wishart (Jensen *et al.* [20]) whereas if other partitions of $\boldsymbol{\varphi}$ involve scalar variance but no covariance components, then the FCD of each component can be shown to be inverted-gamma ([34], [39]).

We subsequently derive the FCD for $\bar{\sigma}^2_{e_k}$ for either the CPMM or the LMM. Under the CPMM,

$$p\left(\bar{\sigma}^2_{e_k} \mid \bar{\sigma}^2_{e_1},\bar{\sigma}^2_{e_2},\ldots,\bar{\sigma}^2_{e_{k-1}},\bar{\sigma}^2_{e_{k+1}},\ldots,\bar{\sigma}^2_{e_s},\delta_1,\delta_2,\ldots,\delta_l,\boldsymbol{\beta},\mathbf{u},\boldsymbol{\varphi},\alpha_e,\mathbf{L},\boldsymbol{\tau},\mathbf{y}\right)$$

$$\propto \left(\prod_{k=1}^{s}\prod_{l=1}^{l}\left(\bar{\sigma}^2_{e_k}\delta_l\right)^{-\frac{n_{kl}}{2}}\right)\exp\left(-\frac{1}{2}\sum_{l=1}^{l}\frac{(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})'(\mathbf{y}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})}{\bar{\sigma}^2_{e_k}\delta_l}\right) \qquad (16)$$

$$\propto \left(\left(\bar{\sigma}^2_{e_k}\right)^{-\frac{\sum_{l=1}^{l}n_{kl}}{2}}\right)\exp\left(-\frac{\sum_{l=1}^{l}\frac{(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})'(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})}{2\delta_l}}{\bar{\sigma}^2_{e_k}}\right)p\left(\bar{\sigma}^2_{e_k}\right)$$

for $k = 1,2,\ldots,s$. Under the LMM, y_{kl} is substituted for L_{kl} and conditioning on $\boldsymbol{\tau}$ and $\mathbf{L}$ is not required in the specification of the FCD of $\bar{\sigma}^2_{e_k}$. With a flat noninformative prior specified for $\bar{\sigma}^2_{e_k}$ (i.e. $p\left(\bar{\sigma}^2_{e_k}\right)\propto 1$, the FCD for $\bar{\sigma}^2_{e_k}$ is then simply inverted gamma with parameters $\alpha_k = \frac{\sum_{l=1}^{l} n_{kl}}{2} - 1$ and $\beta_k = \sum_{l=1}^{l}\frac{(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})'(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})}{2\delta_l}$. It can also be readily shown that if one specifies $p\left(\bar{\sigma}^2_{e_k}\right)$ to be inverted gamma, the FCD of $\bar{\sigma}^2_{e_k}$ will also be inverted gamma.

The FCD of δ_l can be similarly derived:

$$p\left(\delta_l \mid \bar{\sigma}^2_{e_1},\bar{\sigma}^2_{e_2},\ldots,\bar{\sigma}^2_{e_s},\delta_1,\delta_2,\ldots,\delta_{l-1},\delta_{l+1},\ldots,\delta_l,\boldsymbol{\beta},\mathbf{u},\boldsymbol{\varphi},\alpha_e,\mathbf{y},\mathbf{L},\boldsymbol{\tau}\right)$$

$$\propto \left(\prod_{k=1}^{s}\left(\bar{\sigma}^2_{e_k}\delta_l\right)^{-\frac{n_{kl}}{2}}\right)\exp\left(-\frac{1}{2}\sum_{k=1}^{s}\frac{(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})'(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})}{\bar{\sigma}^2_{e_k}\delta_l}\right)$$

$$\frac{(\alpha_e-1)^{\alpha_e}}{\Gamma(\alpha_e)}\left(\delta_l\right)^{-(\alpha_e+1)}\exp\left(-\frac{\alpha_e-1}{\delta_l}\right) \qquad (17)$$

$$\propto \left(\delta_l^{-\left(\frac{\sum_{k=1}^{s}n_{kl}}{2}+\alpha_e+1\right)}\right)\exp\left(-\frac{\sum_{k=1}^{s}\frac{(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})'(\mathbf{L}_{kl}-\mathbf{X}_{kl}\boldsymbol{\beta}-\mathbf{Z}_{kl}\mathbf{u})}{2\bar{\sigma}^2_{e_k}}+\alpha_e-1}{\delta_l}\right)$$

That is, the FCD for δ_l is then simply inverted gamma with shape parameters

$\alpha_l = \frac{\sum_{k=1}^{s} n_{kl}}{2} + \alpha_e$ and scale parameter

$$\beta_l = \sum_{k=1}^{s} \frac{(\mathbf{L}_{kl} - \mathbf{X}_{kl}\boldsymbol{\beta} - \mathbf{Z}_{kl}\mathbf{u})'(\mathbf{L}_{kl} - \mathbf{X}_{kl}\boldsymbol{\beta} - \mathbf{Z}_{kl}\mathbf{u})}{2\bar{\sigma}^2_{e_k}} + \alpha_e - 1 \text{ for } l = 1,2,\ldots,t.$$

The FCD for α_e based on the prior $p(\alpha_e)$ adopted from (10), is

$$\begin{aligned} &\mathrm{p}\left(\alpha_e \mid \boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\varphi}, \bar{\sigma}^2_{e_1}, \bar{\sigma}^2_{e_2}, \ldots, \bar{\sigma}^2_{e_t}, \delta_1, \delta_2, \ldots, \delta_t, \mathbf{y}, \mathbf{L}, \boldsymbol{\tau}\right) \\ &\propto \frac{(\alpha_e - 1)^{\alpha_e t}}{(\Gamma(\alpha_e))^t} \exp\left(-(\alpha_e - 1)\sum_{l=1}^{t} \delta_l^{-1}\right) \prod_{l=1}^{t} (\delta_l)^{-(\alpha_e+1)} p(\alpha_e) \end{aligned} \tag{18}$$

Now (18) is not a recognizable density. We sample from $\psi = \log(\alpha_e)$ using a random walk Metropolis-Hastings sampler with a Gaussian proposal density tuned during MCMC burn-in such that the Metropolis-Hastings acceptance rates are intermediate for optimal MCMC mixing (Chib and Greenberg [4]).

MODEL COMPARISON

The deviance information criterion (DIC) has been recently proposed for comparing goodness of fit for alternative constructions of hierarchical models to data (Speigelhalter *et al.* [36]) and has been increasingly used in animal breeding ([15], [22], [29]). The DIC is based on the posterior distribution of the deviance statistic or -2 times the sampling distribution of the data as specified in the first stage of a hierarchical model. For the LMM, the data sampling stage is specified as:

$$
\begin{aligned}
&p(\mathbf{y} \mid \boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\varphi}, \bar{\sigma}^2_{e_1}, \ldots, \bar{\sigma}^2_{e_s}, \delta_1, \ldots, \delta_t, \mathbf{y}) \\
&= \prod_{k=1}^{s} \prod_{l=1}^{t} (2\pi)^{-\frac{n_{kl}}{2}} (\bar{\sigma}^2_{e_k} \delta_l)^{-\frac{n_{kl}}{2}} \exp\left(\frac{[\mathbf{y}_{kl} - \mathbf{X}_{kl}\boldsymbol{\beta} + \mathbf{Z}_{kl}\mathbf{u}]' \mathbf{R}_{kl}^{-1} [\mathbf{y}_{kl} - \mathbf{X}_{kl}\boldsymbol{\beta} + \mathbf{Z}_{kl}\mathbf{u}]}{2} \right)
\end{aligned}
\qquad (19)
$$

whereas for the CPMM, the data sampling stage is based on further marginalizing the product of (11a) and (11b) across all *n* observations over **L** and is written as follows:

$$
\begin{aligned}
&p(\mathbf{y} \mid \boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\varphi}, \bar{\sigma}^2_{e_1}, \ldots, \bar{\sigma}^2_{e_s}, \delta_1, \ldots, \delta_t, \mathbf{y}) \\
&= \prod_{k=1}^{s} \prod_{l=1}^{t} \prod_{i=1}^{n_{kl}} \Pr ob\left(Y_{ikl} = Y_{ikl} \mid \boldsymbol{\beta}, \mathbf{u}, \boldsymbol{\tau}, \bar{\sigma}^2_{e_1}, \ldots, \bar{\sigma}^2_{e_s}, \delta_1, \ldots, \delta_t \right) \qquad (20) \\
&= \prod_{k=1}^{s} \prod_{l=1}^{t} \prod_{i=1}^{n_{kl}} \left(\Phi\left(\frac{\tau_{Y_{ikl}} - (\mathbf{x}'_{kl}\boldsymbol{\beta} + \mathbf{z}'_{kl}\mathbf{u})}{\sqrt{\bar{\sigma}^2_{e_k} \delta_l}} \right) - \Phi\left(\frac{\tau_{Y_{ikl}-1} - (\mathbf{x}'_{kl}\boldsymbol{\beta} + \mathbf{z}'_{kl}\mathbf{u})}{\sqrt{\bar{\sigma}^2_{e_k} \delta_l}} \right) \right)
\end{aligned}
$$

The DIC is computed as the sum of average Bayesian deviance ($\bar{D}$) plus the "effective number of parameters" (p_D) with respect to a model, such that smaller DIC values indicate better fit to the data. The log marginal likelihood (LML) of the data for a certain model is an alternative model choice criterion that we have adopted in previous research (Kizilkaya *et al.* [22]). Larger values of LML indicate better model fit to the data. We base our LML computations on (19) and (20) in comparing the two respective models. More information about DIC and LML determinations can be found in Speigelhalter *et al.* [36] , Gelfand [10] and Kizilkaya *et al.* [22].

DATA

Simulation Study

A simulation study was carried out to validate Bayesian inference on the proposed heteroskedastic error LMM and CPMM and to assess the ability of the DIC and the LML to correctly choose between homoskedastic and heteroskedastic error GLMM. A simple mixed effects model was used to generate underlying variables liability data **L** for n = 2500 progeny from each of 50 unrelated sires:

$$L_{ijkl} = \mu + sex_i + herd_j + sire_k + e_{ijkl}$$

Here μ=0.5, $\{sex_i\}_{i=1}^{2}$ (sex_1=-0.5 and sex_2=0.5) represents a 2 x 1 vector of fixed sex effects. Furthermore, $\{herd_j\}_{j=1}^{100} \sim N(\mathbf{0},\mathbf{I}\sigma_h^2)$ is a 100 x 1 vector of random effects and $\{sire_k\}_{k=1}^{50} \sim \mathrm{N}(\mathbf{0},\mathbf{I}\sigma_s^2)$ represent a 50x1 vector of independent random effects with σ_h^2=0.25 and σ_s^2=0.10. Finally, $\mathbf{e}_{ij} = \{e_{ijl}\} \sim N(\mathbf{0},\mathbf{I}_{n_{ij}}\bar{\sigma}_{e_i}^2\delta_j)$is the vector of residuals associated with the n_{ij} records from sex *i* and herd *j*. Three replicated datasets from each of four different populations or different values of α_e were generated: Population I) α_e=3, Population II) α_e=12, and Population III) α_e=50 each with $\bar{\sigma}_{e_1}^2$=1, $\bar{\sigma}_{e_2}^2$=1.25 and $\delta_j \sim$ Inverted-Gamma($\alpha_e, \alpha_e - 1$), *j*=1,2….100; and Population IV with homoskedastic error, i.e. α_e=∞ with $\bar{\sigma}_{e_1}^2 = \bar{\sigma}_{e_2}^2$=1 and δ_j=1, *j*=1,2,…,100. The values α_e=3, 12 and 50 represent extreme, moderate and mild levels, respectively, of residual heteroskedasticity across herds. Levels of fixed and random location effects were randomly assigned to individuals in data generation. Augmented data **L** was mapped to ordinal data **y** based on C=4 categories with τ_1=-0.50, τ_2=1.00 and τ_3=2.00 in all populations. Both **L** and **y** were analyzed using the appropriate GLMM (LMM and CPMM, respectively) based on both homogeneous and heterogeneous residual variance structures with flat priors utilized on $\boldsymbol{\beta}$, $\bar{\sigma}_{e_1}^2, \bar{\sigma}_{e_2}^2$, σ_s^2, σ_h^2, and a noninformative prior, as previously described, used for α_e. For the purposes of parameter identifiability, we invoked the restrictions τ_1=-0.50

and $\tau_2 = 1.00$. MCMC was used for Bayesian posterior inference on all parameters. For each replicated data set within each population, a burn-in period of 10,000 cycles was discarded before saving samples from each of an additional 100,000 MCMC cycles. Graphical inspection of the MCMC chains based on preliminary analyses was used to determine a common length of burn-in period. Furthermore, DIC and LML values were computed for each model on each replicated dataset to validate those measures as reliable model choice criteria.

Italian Piemontese Birth Weight and Calving Ease Data

Birth weight and first parity calving ease scores recorded on Italian Piemontese cattle from January, 1989 to July, 1998 by Associazione Nazionale Allevatori Bovini di Razza Piemontese (ANABORAPI), Strada Trinità 32a, 12061 Carrù, Italy were used for this study. As in Kizilkaya *et al.* [22], only herds that were represented by at least 100 records were considered in the study, leaving a total of 8,847 records. Calving ease was scored into five categories by breeders and subsequently recorded by technicians who visited the breeders monthly. The five ordered categories are: 1) unassisted delivery, 2) assisted easy calving 3) assisted difficult calving 4) Caesarean section and 5) foetotomy. As the incidence of foetotomy was less than 0.5%, the last two ordinal categories were combined, leaving a total of four mutually exclusive categories. The general frequencies of first parity calving ease scores in the data set were 951 (10.75%) for unassisted delivery; 5,514 (62.32%) for assisted easy calving; 1,316 (14.88%) for assisted difficult calving; and 1,066 (12.05%) for Caesarean section and foetotomy.

The effects of dam age, sex of the calf, and their interaction were considered by combining eight different age groups (20 to 23, 23 to 25, 25 to 27, 27 to 29, 29 to 31, 31 to 33, 33 to 35, and 35 to 38 months) with sex of calf for a total of 16 nominal subclasses. Herd-year-season (HYS) subclasses were created from combinations of herd, year, and two different seasons (from November to April and from May to October) as in Carnier *et al.* [3] who also analyzed calving ease data from this same population. The sire pedigree file was further pruned by striking out identifications of sires having no daughters with calving ease records and appearing only once as either a sire or a maternal grandsire of a sire having daughters with records in the data file. The number of sires remaining in the pedigree file after pruning was 1,929.

As in Kizilkaya *et al.* [21 22], the LMM and CPMM used for the analyses of birth weight and calving ease data included the fixed effects of age of dam classifications, sex of calf and their interaction in $\boldsymbol{\beta}$, the random effects of independent herd-year-season effects in h, random sire effects in s and random maternal grandsire effects in m. We assume:

$$\begin{pmatrix} \mathbf{s} \\ \mathbf{m} \end{pmatrix} \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A}\right)$$

and

$$\mathbf{h} \sim N\left(\mathbf{0}, \mathbf{I}\sigma_h^2\right)$$

where $\mathbf{G}_0 = \begin{pmatrix} \sigma_s^2 & \sigma_{sm} \\ \sigma_{sm} & \sigma_m^2 \end{pmatrix}$, with σ_s^2 denoting the sire variance, σ_m^2 denoting the maternal grandsire variance, σ_{sm} denoting the sire-maternal grandsire covariance, and σ_h^2 denoting the HYS variance. Furthermore, $\otimes$ denotes the Kronecker product (Searle

[33]), and **A** is the numerator additive relationship matrix between sires due to identified male ancestors (Henderson [14]). Also, **h** is assumed independent of **s** and **m**. Flat priors were placed on all fixed location effects and variance components.

Residual heteroskedasticity was modeled as a function of fixed sex effects ($\bar{\sigma}^2_{e_{male}}$ and $\bar{\sigma}^2_{e_{female}}$) and random herd effects (δ_j, j=1,2,...,66) where δ_j ~ Inverted-Gamma(α_e, α_e-1) in a similar way as in the simulation study. The same flat priors that were considered for fixed dispersion effects and α_e in the simulation study were also considered here.

MCMC inference was based on the running of three different chains for each model. For each chain, a total of 20,000 burn-in cycles followed by saving samples from each of 100,000 additional cycles was generated as previously done in Kizilkaya *et al.* [21 22]. To facilitate diagnosis of MCMC convergence by 20,000 cycles, the starting values on variance components for each chain within a model were widely discrepant, with one chain starting at the posterior mean of all (co)variance components based on a preliminary analysis, another chain starting at the posterior mean minus 3 posterior standard deviations for each (co)variance component and the final chain starting at the posterior mean plus 3 posterior standard deviations for each (co) variance component.

Key genetic parameters, specifically direct heritability (h^2_d), maternal heritability (h^2_m) and the direct-maternal genetic correlation (r_{dm}) were inferred upon in the calving ease data using the transformations on $\mathbf{G}_0$ as considered by Kizilkaya *et al.* [21 22]; however, h^2_d and h^2_m was determined separately for each sex dependent upon the use of either $\bar{\sigma}^2_{e_{Male}}$ or $\bar{\sigma}^2_{e_{Female}}$ in the denominator.

For both the simulation study and the calving ease data analysis, the effective number of independent samples (ESS) was determined using the initial positive sequence estimator of Geyer [11] as adapted by Sorensen *et al.* [34].

RESULTS

Simulation Study

Posterior means and standard deviations and 95% equal-tailed posterior probability intervals (95%PPI) on $\sigma_s^2, \sigma_h^2, \bar{\sigma}_{e_1}^2, \bar{\sigma}_{e_2}^2$ and α_e based on the three replicated datasets from each of the four populations, are provided in Table I for LMM analysis of **L** and Table II for CPMM for the corresponding mapped ordinal values of **y**. For each of the four populations in the simulation study, posterior means of σ_s^2 and σ_h^2 were generally slightly biased upwards for the LMM analysis on **L** and for the CPMM analysis on **y**. Nevertheless, 95% PPIs of these two variance components under both the LMM and CPMM analyses included the true values of parameters in all cases, being understandably wider for the CPMM analysis of **y** due to the substantial loss in data information in mapping from continuous **L** to discrete **y**.

The 95% PPI of $\bar{\sigma}_{e_1}^2$ and $\bar{\sigma}_{e_2}^2$ in both the LMM and CPMM analyses of **L** and **y**, similarly, always included the true values of $\bar{\sigma}_{e_1}^2 = 1$ and $\bar{\sigma}_{e_2}^2 = 1.25$, respectively, for each of the three replicated datasets from each of Populations I, II, and III. Furthermore, for Population IV with homoskedastic error, posterior means and 95% PPIs for $\bar{\sigma}_{e_1}^2$ and $\bar{\sigma}_{e_2}^2$ were found to be similar each other and concentrated around the true value $\bar{\sigma}_{e_1}^2 = \bar{\sigma}_{e_2}^2 = 1$ as anticipated. Also, 95%PPI for α_e inferred on each of the three datasets from each of Populations I, II, and III included the corresponding true parameter value. Posterior standard deviations and widths of 95%PPIs of α_e increased as α_e increased from 3 to 12 to 50 as in Populations I, II, and III, respectively. Furthermore, because of the lower information content of ordinal data relative to underlying liability data, CPMM analyses produced understandably wider 95% PPI and larger standard errors on α_e relative to LMM analyses.

To further validate the residual heteroskedastic GLMM that we propose, the posterior means of each element of $\boldsymbol{\delta}$ as unique for each level of random factor for herd-specific residual variances were compared against the true elements of $\boldsymbol{\delta}$ for each simulation replicate from Populations I, II and III based on LMM and CPMM analyses of **L** and **y**, respectively. The linear relationship between estimated and true values of $\boldsymbol{\delta}$ was estimated based on simple linear regression. We anticipated that as when α_e increased, the linear relationship between posterior means and true values of $\boldsymbol{\delta}$ should approach 0 with greater degree of statistical shrinkage of posterior means to $\boldsymbol{\delta} = 1$. This would be consistent with what is expected with random location effects models where a greater degree of statistical shrinkage is observed when random effects variances are small as opposed to being large (Robinson [31]). The least-squares estimated slopes between posterior means and true values of $\boldsymbol{\delta}$ averaged across each of the three replicates from Populations I, II, and III were 0.882, 0.670 and 0.181, respectively, for the LMM analysis of **L** and 0.669, 0.456 and 0.141, respectively, for the CPMM analysis of **y**, further illustrating the greater degree of shrinkage with the less informative CPMM analysis.

It is important to generate sufficient number of MCMC cycles in order to minimize the impact of Monte Carlo error on posterior inference. Several animal breeders have recently suggested 100 as the minimum effective sample size (ESS) for reliable statistical inference ([2], [37]). In our simulation study, the ESS for $\sigma_s^2, \sigma_h^2, \bar{\sigma}_{e_1}^2, \bar{\sigma}_{e_2}^2$ and α_e ranged from 250-78,000 in LMM for the analysis of **L** and from 160-15,000 in CPMM for the analysis of **y**. As anticipated, the CPMM analysis of **y** was characterized by substantially lower ESS than the LMM analysis of the corresponding **L** from which **y** was mapped via $\boldsymbol{\tau}$; nevertheless, ESS appeared sufficient for reliable posterior inference in both GLMM.

The simulation study was also used to validate DIC and LML as model choice criteria. For this purpose, DIC and LML values for each replicated dataset based on homoskedastic and heteroskedastic GLMM within each of the four populations were determined for the analysis of **L** using a LMM and for the analysis of **y** using a CPMM. A DIC difference exceeding 7 has been suggested by Speigelhalter *et al.* [36] as an indication of a meaningful difference in model fit. The DIC differences between homoskedastic and heteroskedastic GLMM (LMM for **y** and CPMM for **L**) for each matched replicate within populations are shown in Figure 1. In all cases, DIC differences were clearly in favor the correct model. Furthermore, as expected, the magnitude of DIC differences involving LMM analyses of **L** was higher than that for CPMM analyses of **y** since, again, **y** is less informative than **L**. The DIC differences between homoskedastic and heteroskedastic error GLMM approached 0 with increasing α_e.

Application to Birth Weight and Calving Ease Scores in Italian Piemontese Cattle

Genetic Parameter Inference

Sire and maternal grandsire LMM and CPMM were used for the analyses of birth weight and calving ease scores, respectively, in Italian Piemontese cattle. Posterior means and standard deviations, 95% equal-tailed PPI and ESS on dispersion and genetic parameters for birth weight and calving ease scores are summarized in Table III and Table IV, respectively. In all cases, reported inferences were based on combining samples from the three separate MCMC chains after burnin. In addition to the posterior means, the posterior modes and medians (results not reported) using the MCMC algorithm were calculated for each parameter and were found to be very similar to each other, whether for LMM analysis of birth weights or for the CPMM analysis of calving ease scores. These results imply that the posterior densities were symmetric and unimodal.

The total number of ESS for dispersion parameters across the three chains ranged from 1,836 to 21,839 for the LMM analysis of birth weights and from 841 to 14,045 for the CPMM analysis of calving ease scores. As anticipated from the results of the simulation study, the CPMM analysis generated lower ESS than the LMM analysis. Relative to reported results for the homogeneous CPMM in Kizilkaya *et al.* [22], the additional inference on α_e, $\bar{\sigma}^2_{e_{male}}$, and $\bar{\sigma}^2_{e_{female}}$ did not appear to adversely impact MCMC mixing and, subsequently, ESS in the CPMM. We observed similar comparisons in the heteroskedastic versus homoskedastic (results not reported) LMM analysis of birth weights.

For the purposes of model comparison, birth weights were also analyzed using homoskedastic LMM. Estimates of σ_s^2 and σ_m^2 from homoskedastic LMM and CPMM were found to be somewhat higher than the corresponding estimates under the heteroskedastic LMM and CPMM. However, the corresponding 95% PPI for these parameters overlapped considerably between the homoskedastic and heteroskedastic GLMM. Of particular note, the estimate of σ_s^2 using homoskedastic LMM for birth weight was found to be significantly greater than the corresponding estimate in the heteroskedastic LMM since the respective 95% PPI did not overlap whatsoever.

Regardless of the GLMM considered, we observed that the posterior mean of the residual variance from homoskedastic model is nearly equal to the average posterior means of sex-specific residual variances in the heteroskedastic error models. Table III further indicated that the residual variance for male calves is significantly greater than for female calves for birth weight and calving ease scores using LMM and CPMM respectively. This significant difference between residual variances translated into sex-specific differences for direct and maternal heritabilities, as indicated in Table IV. Heteroskedastic LMM and CPMM lead to very low posterior means (<5) for α_e indicating that there is considerable residual heteroskedasticity across herds for both birth weights and calving ease.

Approximate 95% PPI on herd-specific δ_i in the birth weight and calving ease scores analyses were computed and presented in Figure 2 for LMM model and Figure3 for CPMM, respectively. As seen in figures, the PPI for δ_i in many herds do not overlap with the expected average value of 1, indicating that residual variances for these herds is significantly higher or lower than average.

In order to compare the homoskedastic and heteroskedastic LMM (and CPMM) model for fit to the birth weight (and calving ease) datasets, LML and DIC values with its components $\bar{D}$ and p_D are given in Table V. DIC and LML values in Table V were reported separately for each of the three chains under LMM and CPM models. As seen from Table V, DIC and LML results are very consistent within each model indicating small Monte Carlo errors on the DIC and LML differences between homoskedastic and heteroskedastic residual models. Both DIC and LML model choice criteria were in favor of the heteroskedastic LMM and CPM models. Surprisingly, the model complexity, as measured by p_D, was lower for the heteroskedastic LMM model whereas the heteroskedastic CPMM model generated higher model complexity value. Kizilkaya *et al.* [22] analyzed the calving ease data by using homoskedastic cumulative *t*-link model and determined that homoskedastic cumulative *t*-link mixed model (CTMM) was overwhelmingly chosen as the best fitting model choice criteria. However, the DIC and LML comparisons between the heteroskedastic CPMM in this paper and the homoskedastic CTMM in Kizilkaya *et al.* [22], strongly favor the heteroskedastic error CPMM for goodness of fit.

Inference on Sire Effects

Posterior means of elements of **s** were computed under homoskedastic and heteroskedastic error GLMM models, as corresponding point estimates of expected progeny differences (EPD). The relationship between these EPD's were determined by using simple regression and shown in Figure 4 and Figure 6. As seen from figures, there is strong linear relationship between posterior mean estimates of **s**, indicating no reranking problem of sires based on Pearson correlations of 0.97 from LMM and 0.98 from CPM.

The standard errors of prediction were computed as the posterior standard deviation of the MCMC samples of elements of **s**. The scatter plots of these standard errors for both models with the corresponding least squares regression line for the homoskedastic versus heteroskedastic LMM and CPMM models were presented in Figure 5 and Figure 7, respectively. Regression coefficient and correlation between models in birth weight and calving ease analysis were near unity, indicating almost perfect linear relationship between posterior standard errors.

DISCUSSION

There is already extensive animal breeding research dealing with statistical inference on heterogeneous variances based on maximum likelihood or empirical Bayes methods over the last two decades ([6], [8], [9], [16], [18], [19], [30]). In this study, we developed a general framework for structural modeling of heterogeneous residual variances in GLMM based on fully Bayesian inference using MCMC methods. We validated our heteroskedastic GLMM by simulation and applied it to birth weight and calving difficulty data from Italian Piemontese cattle using linear mixed models and cumulative probit mixed models, respectively. Our method could also be conceptually extended to a heteroskedastic analysis of count data based on a Poisson log-normal model or to censored data models (Sorensen *et al.* [35]).

The results from our simulation study indicated that inference on parameters specifying fixed and random sources of residual heteroskedasticity is possible in both linear and threshold mixed models. Furthermore, model choice criteria such as DIC can be used with confidence to assess to choose between heteroskedastic and homoskedastic GLMM specifications.

Residual variances for BW and CE were shown to be greater in male calves compared to female calves in Italian Piemontese cattle, directly resulting in smaller heritabilities of direct and maternal effects for male calves. Furthermore estimates from a homoskedastic specification were midway between the separate male and female posterior mean estimates derived from a heteroskedastic specification. Our results for birth weights are in good agreement with the results from Garrick *et al.* [9]. Ducrocq [6] also estimated 7-18% residual variances in male calves relative to female calves for calving ease scores in Normande and Montbeliarde breeds. Our female calf posterior means of direct and maternal heritabilities were substantially higher than corresponding threshold model estimates with homoskedastic residual assumption for calving ease reported by Manfredi *et al.* [25 26], McGuirk *et al.* [27 28], Varona *et al.* [38], Luo *et al.* [23], Bennett and Gregory [1] and Ducrocq [6]. Direct and maternal heritabilities were also determined to be greater for female than for male calves and differences between them were significant for BW and CE. However, these results should be treated with caution since we did not consider sex-specific inference on genetic variance. This is an area for further research, particularly as the power for inferring upon sex-specific genetic variance is substantially lower than that for residual variance. Inference on strongly negative direct-maternal genetic correlations for BW and CE is in agreement with previous work ([1], [3], [6], [22], [23], [38]).

There appeared to be no appreciable differences in sire re-rankings between homoskedastic and heteroskedastic models. This should be not too surprising if sires are randomly used across lowly and highly variable herds and calf sex ratios within each sire do not deviate appreciably from 50%. However, substantial differences in rerankings might be anticipated using animal models, particularly for across herd rankings of dams.

In the analyses of simulation and field data, two Bayesian model choice criteria DIC and LML, were utilized to choose between homoskedastic and heteroskedastic GLMMs and the homoskedastic GLMM was clearly rejected with small DIC and large LML values. In the analyses of BW and CD datasets in Italian Piemontese cattle, heteroskedastic GLMMs were overwhelmingly chosen as the best fitting models by both model choice criteria. These results and results from previous studies showed the existence of heteroskedastic residual structure and deficiencies of many current genetic evaluation systems.

To further fine-tune genetic evaluation systems, heterogeneous variances could be additionally modeled as a function of age of dam, region or year in models. In addition, heavy-tailed distributions for production traits and liability variables in fitness traits can be jointly modeled with heteroskedastic specifications in GLMM as we are working on currently. Residual and genetic correlations between birth weight and calving difficulty imply that genetic evaluations of calving ease would substantially benefit from a bivariate threshold/linear multiple trait analysis with birth weight ([24], [38]). Further work on providing heteroskedastic modeling options with normal and *t*-distributed specifications involving both traits jointly is needed.

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Table I. Posterior inference on the dispersion and heterogeneity parameters in simulation study using linear mixed effects model.

	σ_s^2		σ_h^2		$\bar{\sigma}_{e1}^2$		$\bar{\sigma}_{e2}^2$		α_e	
Population-Datasets	PM±SD	95%PPI	PM±SD	95%PPI	PM±SD	95%PPI	PM±SD	95%PPI	PM±SD	95%PPI
I-1	0.13±0.03	0.08-0.21	0.24±0.04	0.17-0.33	0.89±0.07	0.76-1.05	1.09±0.09	0.93-1.29	3.32±0.46	2.53-4.33
I-2	0.13±0.03	0.08-0.21	0.31±0.05	0.22-0.42	1.02±0.09	0.87-1.20	1.25±0.10	1.07-1.47	3.27±0.44	2.53-4.24
I-3	0.09±0.02	0.05-0.14	0.33±0.05	0.23-0.45	0.91±0.08	0.78-1.08	1.18±0.10	1.01-1.39	3.37±0.45	2.59-4.37
II-1	0.15±0.04	0.10-0.24	0.24±0.04	0.17-0.34	1.06±0.06	0.95-1.18	1.26±0.07	1.13-1.41	8.65±1.88	5.65-12.93
II-2	0.15±0.04	0.09-0.24	0.28±0.05	0.20-0.39	0.94±0.05	0.84-1.05	1.24±0.07	1.11-1.38	9.21±2.12	5.94-14.11
II-3	0.12±0.03	0.07-0.18	0.34±0.06	0.24-0.47	1.02±0.05	0.92-1.13	1.35±0.07	1.22-1.49	14.83±4.78	8.43-26.67
III-1	0.12±0.03	0.07-0.19	0.23±0.04	0.17-0.33	0.96±0.04	0.88-1.04	1.27±0.06	1.16-1.38	158.62±649.29	21.18-723.67
III-2	0.20±0.05	0.12-0.31	0.32±0.05	0.23-0.44	1.08±0.05	0.99-1.18	1.21±0.05	1.32-1.11	101.49±291.57	19.03-439.30
III-3	0.15±0.04	0.09-0.24	0.32±0.05	0.23-0.44	1.02±0.05	0.93-1.12	1.27±0.06	1.16-1.39	61.39±101.30	17.22-248.24
IV-1	0.16±0.04	0.10-0.25	0.26±0.04	0.18-0.35	1.00±0.04	0.92-1.09	0.98±0.04	0.90-1.06	565.74±2344.53	33.15-3317.27
IV-2	0.11±0.03	0.07-0.18	0.25±0.04	0.18-0.35	1.07±0.05	0.98-1.16	1.05±0.05	0.97-1.14	590.29±2220.86	38.59-3808.86
IV-3	0.12±0.03	0.07-0.19	0.27±0.05	0.19-0.37	1.00±0.04	0.92-1.09	1.00±0.04	0.91-1.09	226.02±912.45	23.00-1267.99

Table II. Posterior inference on the dispersion and heterogeneity parameters in simulation study using cumulative probit mixed model.

	σ_s^2		σ_h^2		$\bar{\sigma}_{e1}^2$		$\bar{\sigma}_{e2}^2$		α_e	
Population-Datasets	PM±SD	95%PPI	PM±SD	95%PPI	PM±SD	95%PPI	PM±SD	95%PPI	PM±SD	95%PPI
I-1	0.15±0.04	0.09-0.23	0.25±0.05	0.17-0.35	0.94±0.09	0.78-1.14	1.15±0.12	0.95-1.41	3.61±0.64	2.59-5.08
I-2	0.13±0.03	0.07-0.20	0.29±0.05	0.20-0.40	1.03±0.10	0.85-1.24	1.12±0.11	0.92-1.36	3.49±0.59	2.55-4.84
I-3	0.09±0.03	0.05-0.15	0.28±0.05	0.19-0.40	0.90±0.10	0.74-1.11	0.94±0.15	0.70-1.27	4.43±0.90	3.02-6.53
II-1	0.13±0.03	0.08-0.21	0.20±0.04	0.14-0.29	0.84±0.07	0.71-0.99	1.08±0.11	0.88-1.32	7.79±2.29	4.61-13.47
II-2	0.16±0.04	0.09-0.26	0.30±0.06	0.20-0.45	1.01±0.10	0.83-1.24	1.54±0.25	1.13-2.11	10.81±4.34	5.65-21.28
II-3	0.12±0.03	0.07-0.19	0.34±0.07	0.23-0.48	1.05±0.09	0.88-1.24	1.24±0.15	1.05-1.65	40.07±105.42	8.90-182.64
III-1	0.11±0.03	0.06-0.18	0.25±0.05	0.17-0.35	0.99±0.06	0.87-1.12	1.33±0.10	1.15-1.53	734.02±6976.83	13.91-2458.94
III-2	0.19±0.05	0.12-0.31	0.31±0.06	0.22-0.43	1.04±0.07	0.91-1.20	1.25±0.09	1.07-1.44	106.37±671.87	10.18-534.80
III-3	0.17±0.05	0.10-0.28	0.36±0.07	0.25-0.51	1.08±0.09	0.92-1.27	1.54±0.16	1.25-1.89	170.09±1575.86	9.78-481.47
IV-1	0.15±0.04	0.09-0.24	0.27±0.05	0.19-0.38	1.02±0.07	0.89-1.15	1.00±0.07	0.87-1.14	725.21±4536.28	24.84-3849.47
IV-2	0.11±0.03	0.06-0.17	0.24±0.04	0.17-0.34	1.07±0.07	0.93-1.22	1.11±0.08	0.96-1.29	138.35±1535.09	9.68-457.73
IV-3	0.14±0.04	0.08-0.23	0.36±0.07	0.24-0.53	1.14±0.12	0.95-1.42	1.36±0.23	1.03-1.91	81.44±387.54	10.12-362.31

Table III. Posterior inference on variance components of birth weight and calving ease scores in Italian Piemontese cattle.

	Linear mixed effects model			Cumulative probit mixed effect model		
Parameter[a]	PM ± SD[b]	95% PPI[c]	ESS[d]	PM ± SD[b]	95% PPI[c]	ESS[d]
σ_s^2	1.128 ± 0.197	0.769 – 1.540	3,379 [1,079 – 1,179]	0.131 ± 0.022	0.091 - 0.178	2,894 [856 – 1,066]
σ_m^2	0.499 ± 0.112	0.305 – 0.739	1,836 [493 – 752]	0.024 ± 0.008	0.010 – 0.042	841 [238 – 345]
σ_{sm}	0.348 ± 0.106	0.145 – 0.563	2,803 [866 – 1,004]	0.024 ± 0.011	0.003 – 0.046	1,169 [362 – 422]
σ_h^2	1.680 ± 0.190	1.326 – 2.072	14,094 [4,273 – 5,367]	0.130 ± 0.016	0.101 – 0.163	7,921 [2,456 – 2,806]
$\bar{\sigma}^2_{e_{Male}}$	14.443 ± 1.029	12.628 – 16.700	7,794 [2,507 – 2,657]	1.0901 ± 0.0919	0.9268 - 1.2898	5,915 [1,960 – 1,987]
$\bar{\sigma}^2_{e_{Female}}$	10.185 ± 0.727	8.894 – 11.769	7,713 [2,458 – 2,650]	0.7103 ± 0.0592	0.606 – 0.839	5,856 [1,936 – 1,966]
$\bar{\sigma}^2_{e_{Male}} - \bar{\sigma}^2_{e_{Female}}$	4.258 ± 0.525	3.291 – 5.357	21,839 [7,025-7,592]	0.3798 ± 0.0533	0.282 – 0.492	14,045 [4,533 – 4,761]
α	4.963 ± 0.850	3.495 – 6.819	18,223 [5,880 – 6,242]	4.0050 ± 0.6744	2.868 – 5.493	13,899 [4,461 – 4,798]
SD(α)	0.600 ± 0.094	0.456 – 0.818	16,841 [5,442 – 5,842]	0.7397 ± 0.1414	0.535 – 1.073	13,044 [4,146 – 4,685]

[a] See text for description.

[b] Posterior mean ± standard deviation.

[c] 95% equal-tailed posterior probability interval.

[d] The total effective number of independent samples across the three MCMC chains using the initial positive sequence estimator of Geyer (1992).; interval values [ ] refer to range in ESS across the three chains.

Table IV. Posterior inference on genetic parameters of birth weight and calving ease scores in Italian Piemontese cattle.

	Linear mixed effects model			Cumulative probit link mixed model		
Parameter[a]	PM ± SD[b]	95% PPI[c]	ESS[d]	PM ± SD[b]	95% PPI[c]	ESS[d]
$h^2_{D\_Male}$	0.245 ± 0.043	0.167 – 0.333	3,392 [1,069-1,181]	0.370 ± 0.064	0.255 – 0.503	2,687 [813-949]
$h^2_{M\_Male}$	0.094 ± 0.027	0.050 – 0.153	1,617 [455-618]	0.092 ± 0.033	0.040 – 0.167	943 [231-363]
$h^2_{D\_Female}$	0.318 ± 0.054	0.219 – 0.430	3,315 [1,041-1,159]	0.504 ± 0.083	0.351 – 0.678	2,488 [740-893]
$h^2_{M\_Female}$	0.122 ± 0.035	0.065 – 0.199	1,610 [452-616]	0.126 ± 0.045	0.054 – 0.228	935 [230-360]
r_{DM}	-0.302 ± 0.151	-0.567 – 0.019	2,328 [747-811]	-0.629 ± 0.146	-0.886 - -0.207	975 [302-350]
$h^2_{D\_Female} - h^2_{D\_Male}$	0.073 ± 0.014	0.048 – 0.102	4,354 [1,371-1,529]	0.134 ± 0.025	0.089 – 0.187	3,093 [916-1,131]
$h^2_{M\_Female} - h^2_{M\_Male}$	0.028 ± 0.009	0.015 – 0.047	1,819 [506-704]	0.034 ± 0.013	0.014 – 0.063	1,025 [260-394]

[a] See text for description.

[b] Posterior mean ± standard deviation.

[c] 95% equal-tailed posterior probability interval.

[d] The total effective number of independent samples across the three MCMC chains using the initial positive sequence estimator of Geyer (1992).; interval values [ ] refer to range in ESS across the three chains.

Table V. MCMC chain-specific deviance information criterion (DIC) and log marginal likelihood (LML) values for the analysis of birth weight and calving ease scores in Italian Piemontese cattle.

	$\bar{D}$[a]	$D(\bar{\theta})$[b]	P_D[c]	*DIC*	LML
			LMM		
Homoskedasticity					
Chain 1	45,930	44,994	936	46,866	-23,474
Chain 2	45,930	44,994	936	46,866	-23,474
Chain 3	45,930	44,994	936	46,866	-23,474
Heteroskedasticity					
Chain 1	45,240	44,332	908	46,148	-23,189
Chain 2	45,239	44,331	908	46,147	-23,188
Chain 3	45,240	44,331	909	46,149	-23,189
			CPMM		
Homoskedasticity					
Chain 1	16,564	15,782	782	17,346	-8,705
Chain 2	16,562	15,780	782	17,344	-8,705
Chain 3	16,562	15,779	783	17,345	-8,705
Heteroskedasticity					
Chain 1	15,949	15,145	804	16,753	-8,425
Chain 2	15,948	15,143	805	16,753	-8,425
Chain 3	15,948	15,144	805	16,753	-8,425

[a] The average of Bayesian deviance.

[b] Bayesian deviance based on posterior mean vector.

[c] The effective number of parameters.

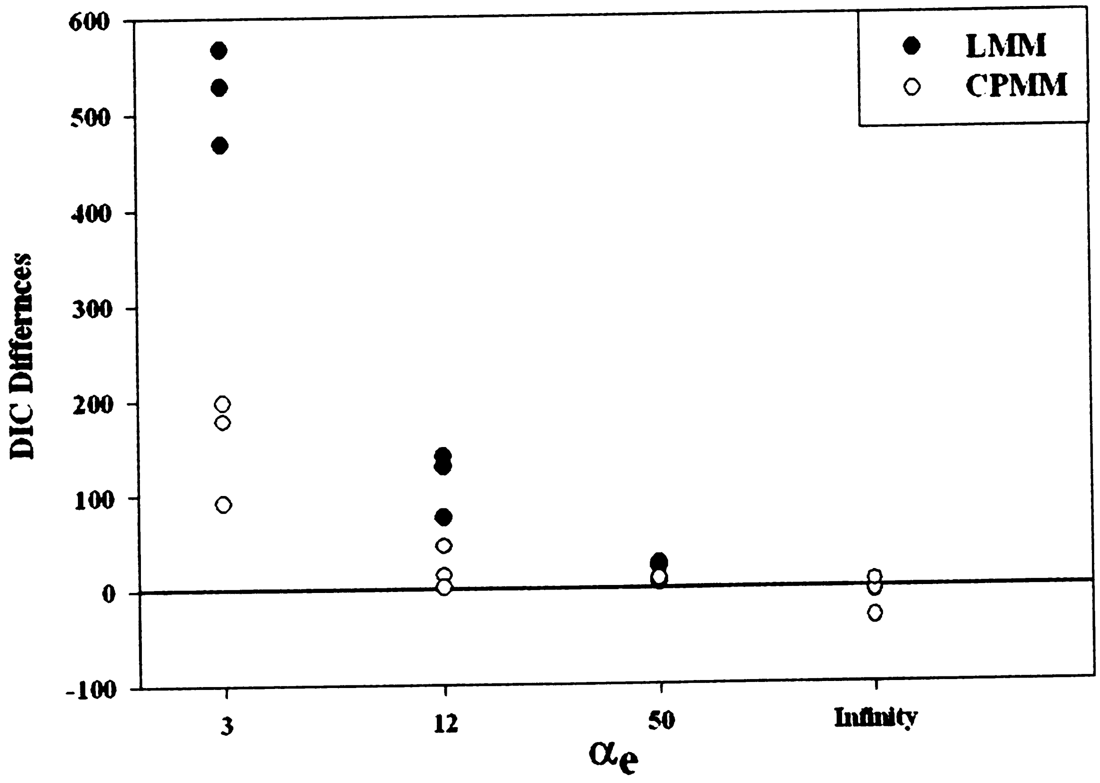

Figure 1. DIC differences in simulation study.

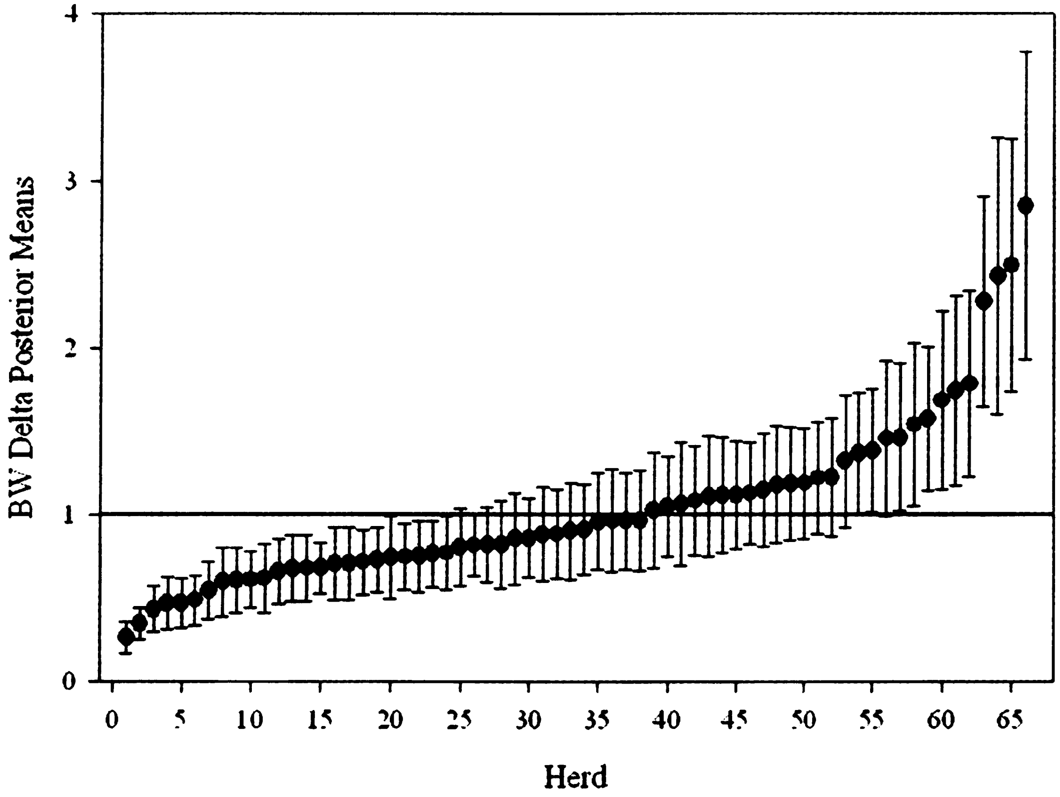

Figure 2. Approximate 95% PPI on herd-specific delta for BW.

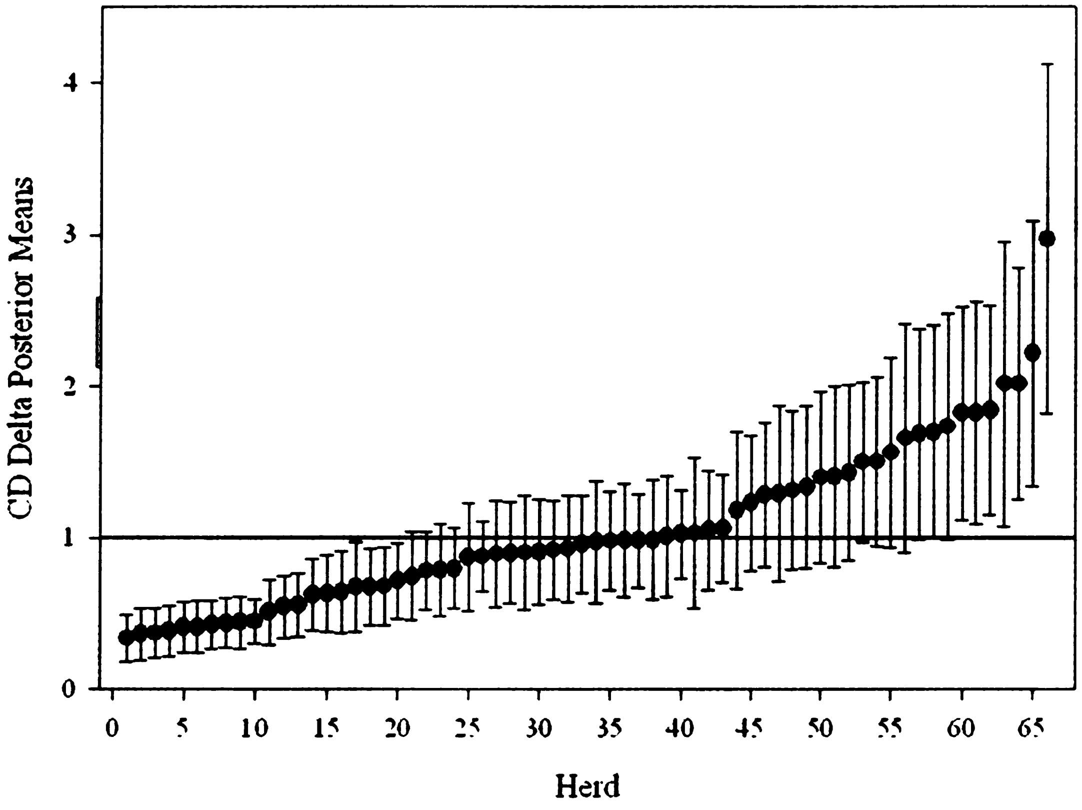

Figure 3. Approximate 95% PPI on herd-specific delta for CE.

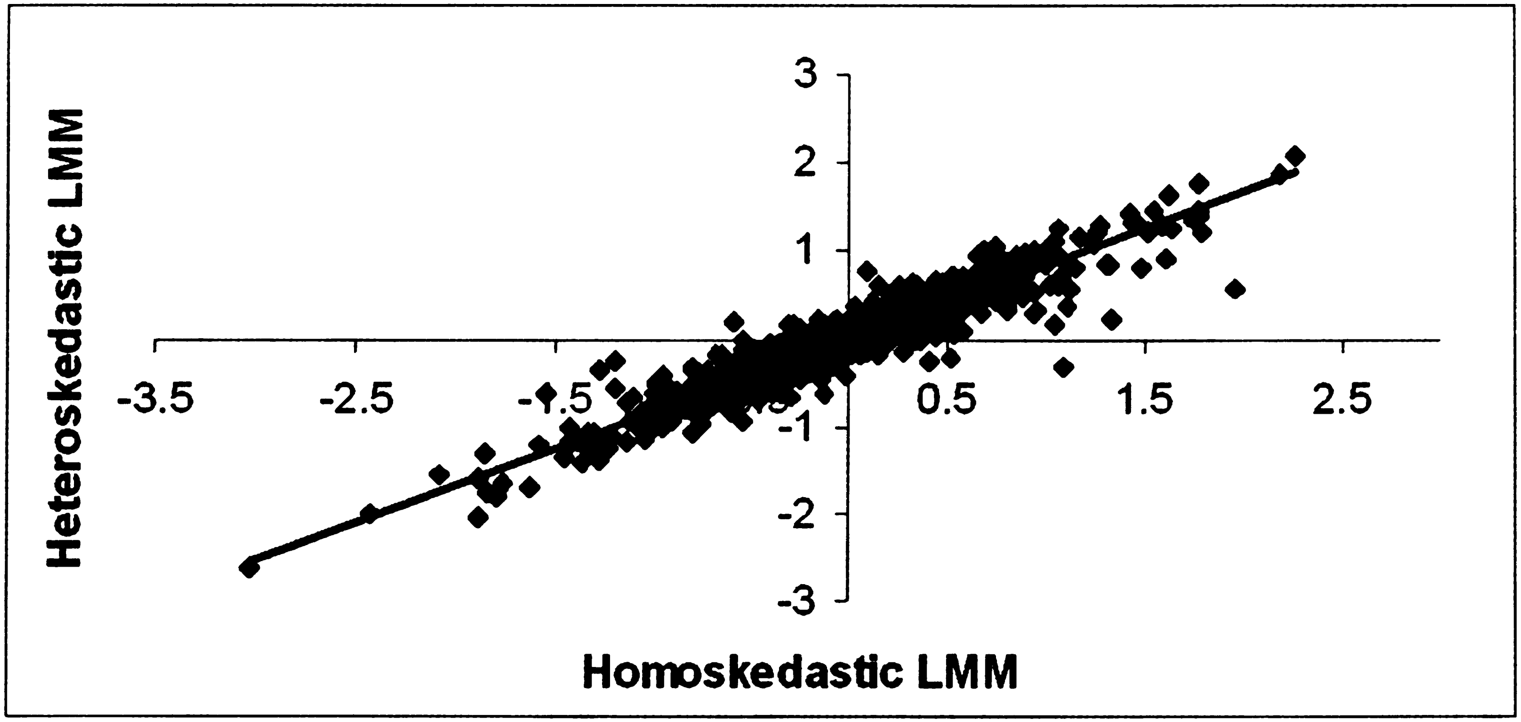

Figure 4. Scatterplot of posterior means of sire progeny differences for BW based on homoskedastic versus heteroskedastic LMM model.

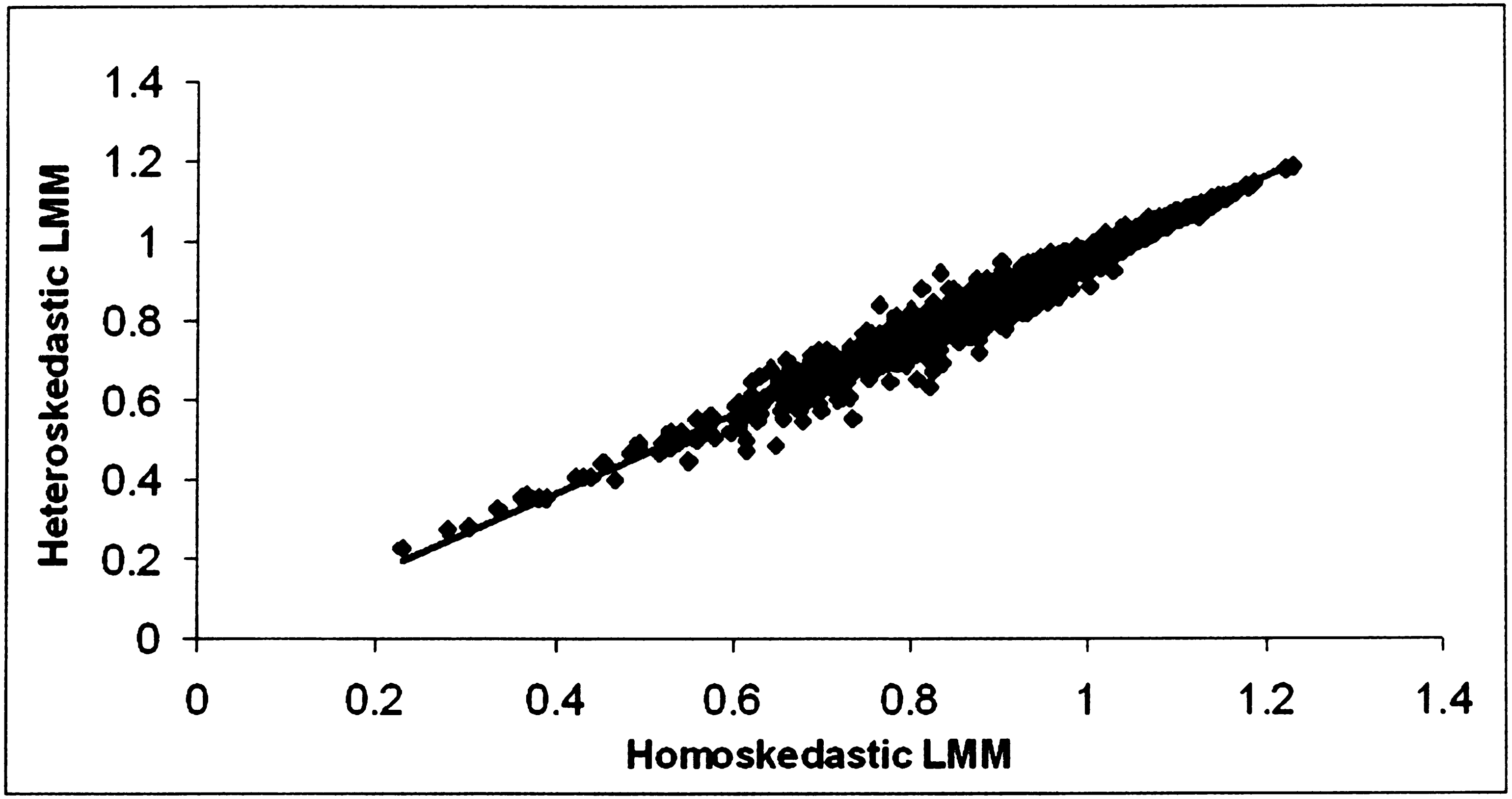

Figure 5. Scatterplot of posterior standard deviations of sire progeny differences for BW based on homoskedastic versus heteroskedastic LMM model.

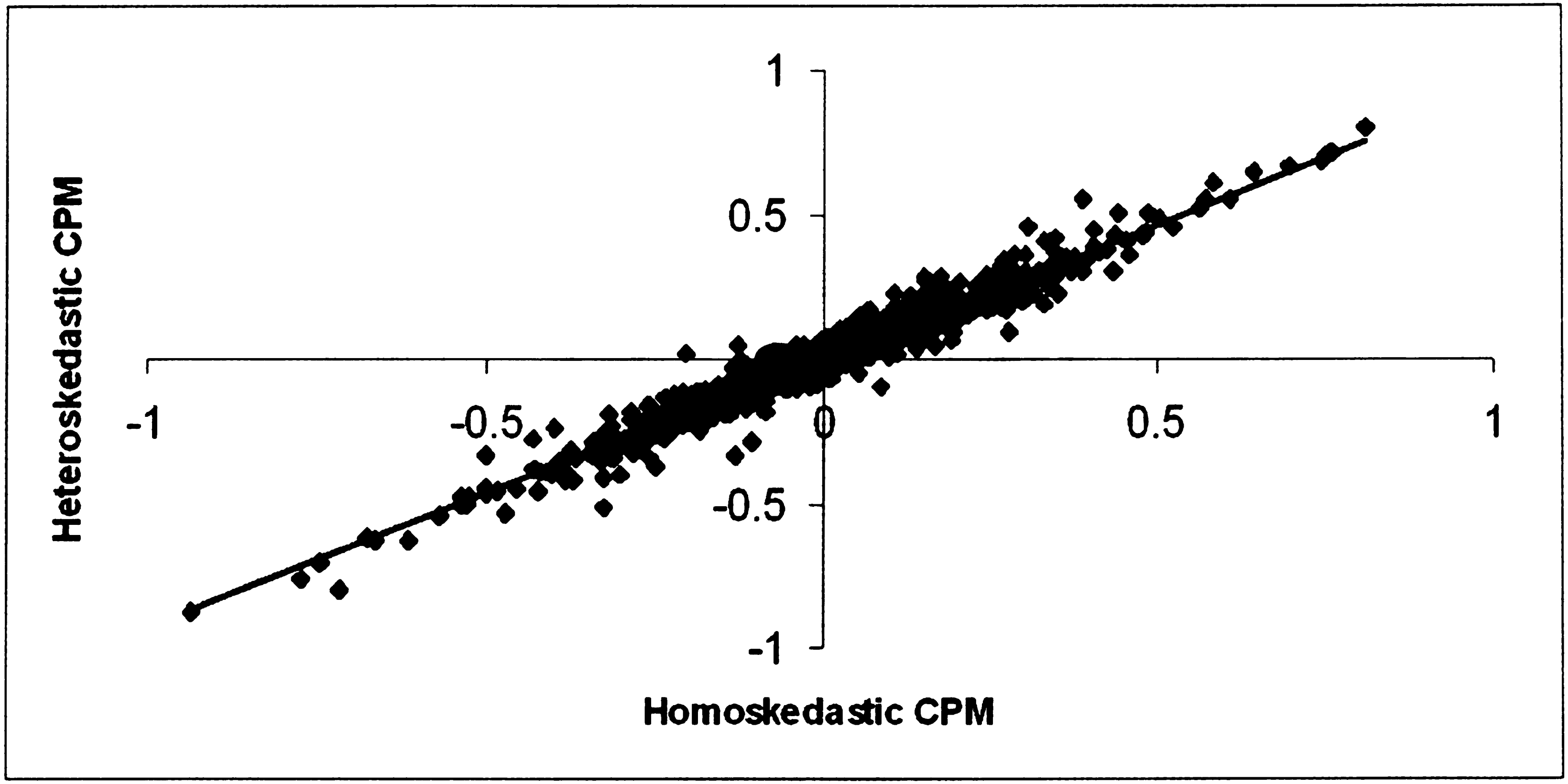

Figure 6. Scatterplot of posterior means of sire progeny differences for CE based on homoskedastic versus heteroskedastic CPM model.

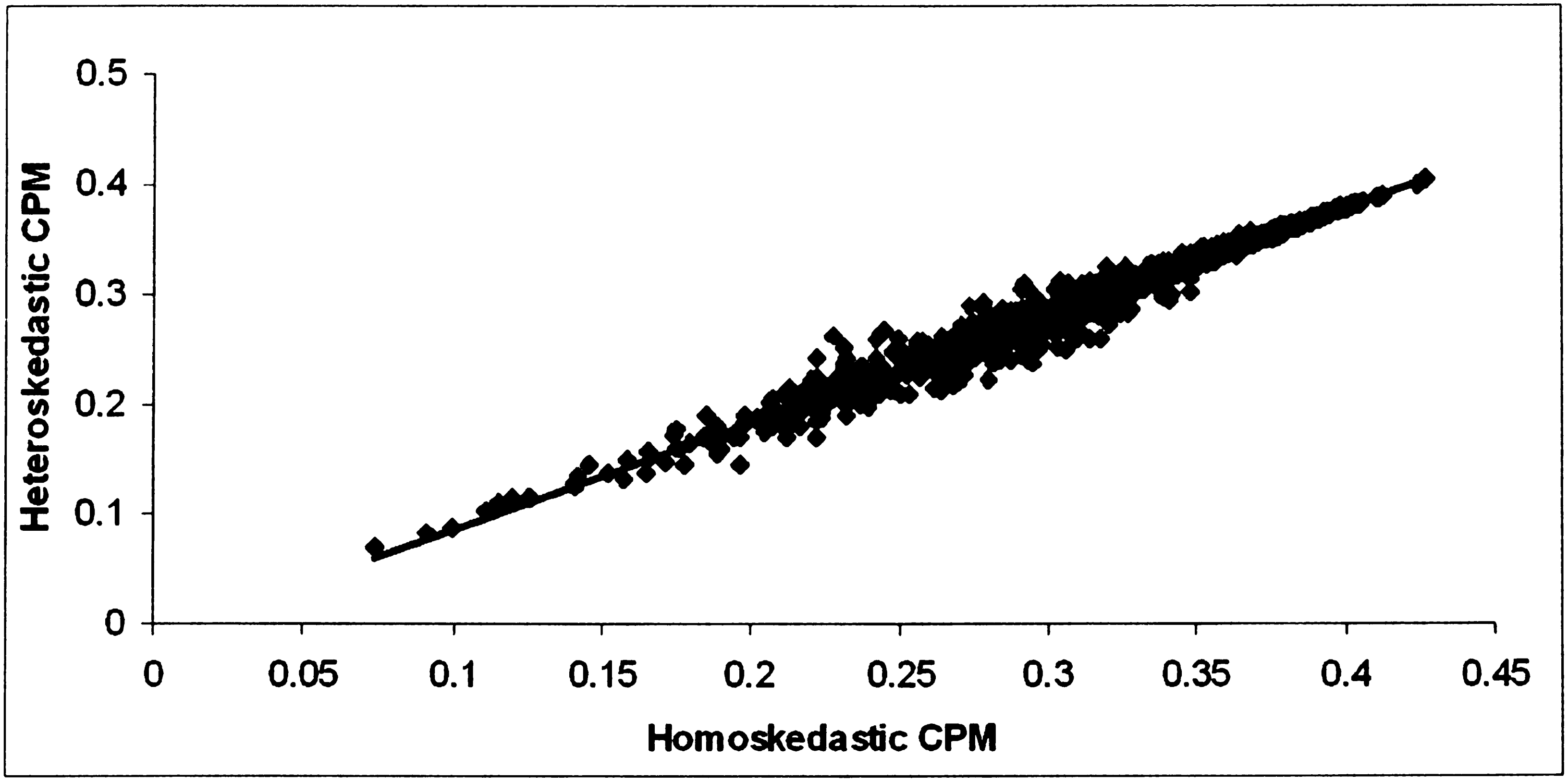

Figure 7. Scatterplot of posterior standard deviations of sire progeny differences for CE based on homoskedastic versus heteroskedastic CPM model.

CONCLUSIONS AND RECOMMENDATIONS

Fitness traits such as conformation score, calving ease and ovulation rate affect livestock production profitability. This fact has been reflected in animal breeding as selection emphasis has shifted gradually away from yield to fitness traits in order to maximize farm income. Calving ease is particularly important for cost control to beef and dairy cattle production because of the increased risk that calving problems add to the survival of both calf and dam. Accurate inference on genetic parameters and genetic merit are important for effective sire selection strategies to improve calving ease.

Variance components and their derivative genetic parameters in a threshold sire-maternal grandsire model analysis of calving ease have been historically estimated using approximate marginal maximum likelihood (MML) procedures based on expectation-maximization (EM). In order to assess the validity of approximate MML estimates, inferences were compared to those based on sequences of Markov Chain Monte Carlo (MCMC) sampling in Chapter II. Laplacian MML and MCMC point estimates of variance components and direct and maternal heritabilities were found to be significant for calving ease in first parity Italian Piemontese dams. However, the covariance between additive direct and maternal effects was found to be not different from zero based on MCMC-derived posterior probability intervals. Furthermore, the joint modal estimates of sire effects and associated standard errors based on MML estimates of variance components differed little from the respective posterior means and standard deviations using MCMC. The results suggest that it may not be necessary to apply computationally intensive MCMC methods for inferences on genetic parameters and sire genetic merits using threshold models on large calving ease data sets, at least based on a conventional genetic evaluation model.

A hierarchical threshold mixed model based upon a cumulative *t*-link rather than a cumulative probit link specification for the analysis of ordinal data was developed and applied to calving ease scores in Chapter III. The model and MCMC algorithm were validated on simulated liability and categorical data sets from normal and *t* distributions (with 4 degrees of freedom) using the deviance information criterion (DIC) and log marginal likelihood (LML). The simulation study indicated that inference on the *t* error degrees of freedom was reliable for the analyses of liability and ordinal data sets; however, MCMC mixing was problematic, especially for ordinal data. Both DIC and LML were able to choose the correct model in most cases. In the analysis of calving ease scores on Italian Piemontese cattle, the cumulative *t*-link model was overwhelmingly chosen as the best fitting model. However, the posterior means of direct and maternal heritabilities from cumulative probit link and *t*-link threshold models were found to be not meaningfully different from each other. Furthermore, the examination of posterior means of sire effects showed that there was no real difference between two models in terms of genetic rankings of sires. A surprising result is that the covariance between additive direct and maternal effects was found to be significantly negative in Chapter III, in stark contrast to the results presented in Chapter II. The result in Chapter II further appeared to be dependent upon whether or not herds were treated as random or fixed.

In Chapter IV, a Bayesian hierarchical generalized mixed model based on a structural multifactorial model with fixed and random effects that multiplicatively influence heterogeneity of residual variance was developed. The models and MCMC algorithms were validated on simulated normal and ordinal categorical data characterized by heteroskedastic residual structures. The simulation study further indicated that DIC and LML were useful in correctly choosing between heteroskedastic and homoskedastic models. Application of the method on Italian Piemontese calving ease data indicated that the residual variance for male calves was significantly greater than that for female calves; and that residual variances for some herds were significantly higher or lower than average. However, as in Chapter 2, the high correlation between posterior mean of sire effects from heteroskedastic and homoskedastic models suggested no meaningful reranking.

It appears that better hierarchical Bayesian models confer primary advantages in more accurately modeling variability in calving ease without providing major perturbations on sire rankings. Whereas this may be true for cumulative probit mixed effects models, this is less likely to be the case for linear mixed effects models, as hinted by a heteroskedastic analysis of birth weight in Chapter IV. Furthermore, significant rerankings may be expected to occur in animal model rather than sire model specifications, particularly for dams.

In future research, heterogeneous residual variance could be modeled as a function of age of dam, year or region as further extensions to the models considered in Chapter IV. Furthermore, heteroskedastic *t*-error based mixed models for residuals might be considered for the analyses of production and liability variables; work is already underway on this front with preliminary results indicating heteroskedastic t-error models as the best fitting relative to those models considered in this dissertation.

More significantly, heterogeneity of residual and genetic correlations might exist between birth weight and calving difficulty. As this phenomenon potentially influences national selection strategies, further work on providing greater modeling flexibility with normal and *t*-distributed homoskedastic and heteroskedastic error structures on both traits jointly is needed.