

Sire Evaluation of Count Traits with a Poisson-Gamma Hierarchical Generalized Linear Model

C. Lee¹ and Y. Lee²

Laboratory of Statistical Genetics, Institute of Environment & Life Science, Hallym University
Chuncheon, Kangwon-do 200-702, Korea

ABSTRACT: A Poisson error model as a generalized linear mixed model (GLMM) has been suggested for genetic analysis of counted observations. One of the assumptions in this model is the normality for random effects. Since this assumption is not always appropriate, a more flexible model is needed. For count traits, a Poisson hierarchical generalized linear model (HGLM) that does not require the normality for random effects was proposed.

In this paper, a Poisson-Gamma HGLM was examined along with corresponding analytical methods. While a difficulty arises with Poisson GLMM in making inferences to the expected values of observations, it can be avoided with the Poisson-Gamma HGLM. A numerical example with simulated embryo yield data is presented.

(Key Words: Generalized Linear Mixed Model, Hierarchical Likelihood)

INTRODUCTION

Various quantitative genetic analyses of non-normal data have been extended from Hendersonian mixed linear model methodology. For instance, ordinary categorical traits such as dystocia were analyzed with threshold models (Gianola and Foulley, 1983; Harville and Mee, 1984; Zhao, 1987). A probit link function was recommended for analysis of a Bernoulli variable such as survival data (Foulley et al., 1987; Everett, 1996). Poisson models have been suggested for counted variates, e.g. litter size (Foulley et al., 1987), prolificacy (Perez-Enciso et al., 1993), and embryo yield (Tempelman and Gianola, 1994).

All the analyses mentioned above had a linear aspect in the systematic part of the analytical model, and these models may be categorized as generalized linear mixed models (GLMM). In this class of models, observations can have errors from some exponential family. However, random components are assumed to be normal.

Recently, Lee and Nelder (1996) proposed substantially flexible models called the hierarchical generalized linear models (HGLM). In the models, the normality for random effects is no longer a restriction, and the distribution of these effects may be arbitrary.

In this paper, it is maintained that HGLM can be utilized for analysis of counted traits because it satisfies the following assumptions: the phenotypes have a Poisson

distribution, and a Gamma distribution is used for random effects. It has been known that Poisson or Negative Binomial distributions are suitable to analyze counted traits (Foulley et al., 1987; Perez-Enciso et al., 1993; Tempelman and Gianola, 1994). One of the choices for the distribution of random effects is a conjugate family. So, if the observations conditional on random components are assumed to have a Poisson distribution, then the distribution for the random effects is Gamma. This model is defined as the Poisson-Gamma HGLM. As a specific case, the Poisson-Gamma HGLM only with an intercept and random effects leads to the Negative Binomial model.

The objective of this study was to derive a Poisson-Gamma HGLM for sire evaluation. This involves a formulation of hierarchical likelihood function and a procedure for estimating fixed effects, random effects, and dispersion parameters in the model. A numerical example with a simulated data set is presented.

AN OVERVIEW OF HIERARCHICAL GENERALIZED LINEAR MODELS

Explained here are the HGLM of Lee and Nelder (1996) and its corresponding likelihood called hierarchical likelihood. This likelihood is an expansion of Henderson's (1975) joint likelihood to non-normal mixed models.

Hierarchical generalized linear models

Let y be the observable response variable and u be the unobservable random effect. First, the conditional log-likelihood for y given u is assumed as

* This research was supported by the Korea Research Foundation, Project No. 1997-003-G00025.

¹ Address reprint requests to C. Lee.

² Department of Statistics, Seoul National University, Seoul 151-742, Korea

Received October 23, 1997; Accepted June 3, 1998

$$l(\theta', \phi; y|u) = \{y\theta' - b(\theta')\}/a(\phi) + c(y, \phi)$$

where a , b , and c are known functions, and θ' and ϕ are the canonical and dispersion parameters, respectively. The conditional mean and variance are $E(y|u) = \mu'$ and $\text{var}(y|u) = \phi V(\mu')$ where $\eta' = g(\mu')$ with a generalized linear model (GLM) link function, g . The linear predictor η' takes the form

$$\eta' = \eta + Zv$$

where $\eta = X\beta$ as for a GLM of Nelder and Wedderburn (1972) and $v = v(u)$ for some strictly monotonic function of u .

Secondly, the distribution of u is assumed appropriately from an arbitrary density. Most researchers in this area assumed that the distribution of v is Normal (Westell, 1984; Foulley et al., 1987; Zhao, 1987; Breslow and Clayton, 1993; Foulley and Im, 1993; Perez-Enciso et al., 1993; Tempelman and Gianola, 1994; Klei, 1995; Lee and Pollak, 1997). The normality assumption is convenient when the random effects, v , are correlated. However, the distribution of v , or equivalently u , is better decided by the properties of data or the purposes of inference.

Hierarchical likelihood

The hierarchical likelihood is defined as;

$$h = l(\theta', \phi; y|v) + l(\alpha; v),$$

where $l(\theta', \phi; y|v)$ is the log-density function for y given v , and $l(\alpha; v)$ is the log-density function for v with parameter α . This likelihood is the logarithm of the joint density function for y and v . This reduces to Henderson's joint likelihood under the normality of both $y|v$ and v . The hierarchical likelihood is not an orthodox likelihood because v are unobservable.

The estimators and predictors can be derived by maximizing the hierarchical likelihood, i.e., the estimates are obtained by solving $\partial h / \partial \beta = 0$ and $\partial h / \partial v = 0$. The use of hierarchical likelihood avoids the integration required for marginal likelihood.

A POISSON-GAMMA HIERARCHICAL GENERALIZED LINEAR MODEL

A poisson-gamma model

An HGLM with one fixed effect and one random effect was considered to evaluate genetic merit of sires without their relationship. Suppose that the conditional distribution of a counted variate y_{ijk} given u_{ij} has the

Poisson distribution with Poisson parameter $\lambda_{ij} = \mu'_{ij} = \mu_i u_{ij}$ i.e.,

$$f_1(y_{ijk}|u_{ij}) = e^{-\lambda_{ij}} \lambda_{ij}^{y_{ijk}} / y_{ijk}!$$

$y_{ijk} = 0, 1, \dots$; $i = 1, 2, \dots, n_i$; $j = 1, 2, \dots, n_j$; $k = 1, 2, \dots, n_k$; $\lambda_{ij} \geq 0$.

Then the conjugate HGLM is

$$\eta'_{ij} = \ln \mu'_{ij} = \ln \mu_i + \ln u_{ij} = \mu_i + v_{ij} = \mu + \beta_i + v_{ij},$$

where $\eta = X\beta$ and $v_i = \log u_i$. Assumed is a constraint on u such as $E(u_i) = 1$, a conjugate density for u is a gamma distribution with shape parameter α such that

$$f_2(u_{ij}) = \alpha^\alpha u_{ij}^{\alpha-1} e^{-\alpha u_{ij}} / \Gamma(\alpha).$$

Then the hierarchical log likelihood is constructed by summing the logarithms of the density functions shown above;

$$\begin{aligned} h &= l(\theta', \phi; y|v) + l(\alpha; v) \\ &\propto \sum_{ijk} (y_{ijk} \ln \lambda_{ij} - \lambda_{ij}) + \sum_{ij} \{ \alpha v_{ij} + \alpha \ln \alpha - \alpha u_{ij} - \ln \Gamma(\alpha) \}. \end{aligned}$$

In order to estimate fixed and random effects given parameters, the first derivatives against those effects are first derived as follows:

$$\begin{aligned} \partial h / \partial \mu &= \sum_{ijk} (y_{ijk} - \mu'_{ij}); \\ \partial h / \partial \beta_i &= \sum_{jk} (y_{ijk} - \mu'_{ij}); \\ \partial h / \partial v_{ij} &= \sum_k (y_{ijk} - \mu'_{ij}) + \alpha (1 - e^{v_{ij}}). \end{aligned}$$

And the second derivatives are calculated:

$$\begin{aligned} \partial^2 h / \partial \mu^2 &= -\sum_{ijk} \mu'_{ij}; \\ \partial^2 h / \partial \beta_i^2 &= -\sum_{jk} \mu'_{ij}; \\ \partial^2 h / \partial v_{ij}^2 &= -(\sum_k \mu'_{ij} + \alpha e^{v_{ij}}); \\ \partial^2 h / \partial \mu \partial \beta_i &= -\sum_{jk} \mu'_{ij}; \\ \partial^2 h / \partial \mu \partial v_{ij} &= -\sum_k \mu'_{ij}; \\ \partial^2 h / \partial \beta_i \partial v_{ij} &= -\sum_k \mu'_{ij}; \\ \partial^2 h / \partial \beta_i \partial v_{i'j'} &= 0 \text{ when } i \neq i'; \\ \partial^2 h / \partial v_{ij} \partial v_{i'j'} &= 0. \end{aligned}$$

The corresponding expected Hessian matrix can be written as;

$$H = \begin{pmatrix} X^T W X & X^T W Z \\ Z^T W X & Z^T W Z + U \end{pmatrix},$$

where W is the GLM weight function, $W = (\partial \mu' / \partial \eta')^2 v$

$(\mu')^{-1}$ and U is a diagonal matrix with j^{th} element $-\Phi\{\partial^2 l(\alpha; v)/\partial v_j^2\}$,

$$= \begin{bmatrix} -\frac{\partial^2 h}{\partial \mu^2} & -\frac{\partial^2 h}{\partial \mu \partial \beta_1} & \dots & -\frac{\partial^2 h}{\partial \mu \partial \beta_{i-1}} & -\frac{\partial^2 h}{\partial \mu \partial v_{1,1}} & -\frac{\partial^2 h}{\partial \mu \partial v_{1,2}} & \dots & -\frac{\partial^2 h}{\partial \mu \partial v_{1,n}} \\ -\frac{\partial^2 h}{\partial \beta_1^2} & \dots & -\frac{\partial^2 h}{\partial \beta_1 \partial \beta_{i-1}} & -\frac{\partial^2 h}{\partial \beta_1 \partial v_{1,1}} & \dots & -\frac{\partial^2 h}{\partial \beta_1 \partial v_{1,n}} & 0 & \dots & 0 & \dots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots \\ -\frac{\partial^2 h}{\partial \beta_{i-1}^2} & 0 & \dots & 0 & \dots & 0 & -\frac{\partial^2 h}{\partial \beta_{i-1} \partial v_{1,1}} & \dots & -\frac{\partial^2 h}{\partial \beta_{i-1} \partial v_{1,n}} \\ \text{sym.} & -\frac{\partial^2 h}{\partial v_{1,1}^2} & 0 & \dots & \dots & 0 & \vdots & \vdots & 0 & -\frac{\partial^2 h}{\partial v_{1,n}^2} \\ & -\frac{\partial^2 h}{\partial v_{1,2}^2} & \ddots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \end{bmatrix}$$

Let $(\beta^{(k)}, v^{(k)})'$ be a k^{th} solution vector. Then this vector can be solved by the Newton-Raphson method as follows.

$$\begin{pmatrix} \beta^{(k+1)} \\ v^{(k+1)} \end{pmatrix} = \begin{pmatrix} \beta^{(k)} \\ v^{(k)} \end{pmatrix} + (H^{(k)})^{-1} \begin{pmatrix} \frac{\partial h}{\partial \beta} \\ \frac{\partial h}{\partial v} \end{pmatrix} \bigg|_{\substack{\beta = \beta^{(k)} \\ v = v^{(k)}}}$$

In every round, $(k+1)^{\text{th}}$ solutions satisfy the above equation. Iterations continue until solutions are converged. The resulting solutions have the following properties: $\hat{\mu}_{ij} = (y_{ij+} + \alpha) / (\hat{\mu}_{ij+} + \alpha)$ where $y_{ij+} = \sum_k y_{ijk}$ and $\mu_{ij+} = \sum_k \mu_{ijk}$, is the best linear unbiased predictor, and $\hat{\beta}$ is marginal maximum likelihood estimator.

Scaled deviance test

The scaled deviance is defined as;

$$D(y, \hat{\mu}') = -2 \{l(\hat{\mu}', \Phi; y|v) - l(y, \Phi; y|v)\}$$

with the estimated degrees of freedom n -trace $(H^{-1}H^*)$, where H^* is a modified H excluding the matrix U in the last block diagonal part. The scaled deviance test is performed by comparing the scaled deviance with the degree of freedom; if the former is much larger than the latter, then we may suspect the absence of some necessary fixed effects, random effects, or overdispersion in the $y|v$ distribution.

Estimation of dispersion parameters

One of the major interests in the models with random effects is to develop better methods that estimate dispersion parameter for random and error components. Along with MLM, Patterson and Thompson's (1971) restricted maximum likelihood (REML) has been employed to estimate variance components. Breslow and Clayton (1993) extended this approach to GLMM by using the normal likelihood. In HGLM, Lee and Nelder (1996) introduced the maximum adjusted profile hierarchical likelihood estimator (MAPHLE). Adjusted hierarchical likelihood is defined as follows;

$$h_A = h + .5 \ln \{ \det(2\pi \Phi H^{-1}) \}.$$

Then the adjusted profile hierarchical likelihood is

$$h_p = h_A |_{\beta = \hat{\beta}, v = \hat{v}},$$

where $\hat{\beta}$ and \hat{v} are estimated values. The first and the second derivatives against α are derived:

$$\begin{aligned} \frac{\partial h_A}{\partial \alpha} &= \sum_{ij} (v_{ij} - u_{ij} + \ln \alpha + 1 - \frac{d}{d\alpha} \ln \Gamma(\alpha)) - \\ &\quad \frac{1}{2} \text{tr} (H^{-1} \frac{\partial H}{\partial \alpha}) \end{aligned}$$

$$\frac{\partial^2 h_A}{\partial \alpha^2} = \sum_j \left(\frac{1}{\alpha} - \frac{d^2}{d\alpha^2} \ln \Gamma(\alpha) \right) + \frac{1}{2} \text{tr} \left(H^{-1} \frac{\partial H}{\partial \alpha} \right)$$

Let the Hessian matrix $H_p = -\partial^2 h_A / \partial \alpha^2$. Then the MAPHLEs for dispersion parameters can be obtained by iteratively solving the equation below:

$$\alpha^{(k+1)} = \alpha^{(k)} + (H_p^{(k)})^{-1} \left(\frac{\partial h_A}{\partial \alpha} \right) \bigg|_{\alpha = \alpha^{(k)}}$$

The MAPHLE becomes the REML estimator in mixed linear models, so that it is the generalization of the REML estimator to non-normal mixed models.

NUMERICAL EXAMPLE

Simulation

A simulation was performed to illustrate the procedure

for sire evaluation with the Poisson-Gamma HGLM. Simulated were embryo yields within a nucleus scheme. An embryo yield was generated with a Poisson parameter (λ_{ij}) whose logarithm was additively explained by fixed and random effects. The fixed effects had two levels. The underlying means on the log scale were $\ln(6)$ and $\ln(9)$ for the two levels.

Thirty sire of dam random effects were generated from the gamma distribution with shape parameter equal to 5, and the sires were assumed to be unrelated. However, the use of the sire of dam effects might be vulnerable because genetic effects for embryo yields were not significant in previous studies (Lohuis et al., 1990; Hahn, 1992). Since service sire effects were an important source of variation for embryo yield (Lohuis et al., 1990; Hasler, 1992), the generated random effects could be considered as the unrelated service sire effects.

All the random deviates from Poisson and Gamma distributions were generated with the algorithms by Press et al. (1992). The simulated data by fixed and random effects are shown in table 1. Each sire had 10 female

Table 1. Simulated embryo yields by fixed and random effects

Fixed effects	Random effects			Embryo yields within effects							
1	1	6	7	10	5	6	14	8	7	2	13
	2	5	6	7	3	8	5	9	6	5	5
	3	7	9	13	9	12	12	9	8	4	13
	4	4	2	7	7	4	3	2	6	1	3
	5	11	1	1	4	3	5	1	5	4	4
	6	9	3	12	6	6	7	4	6	7	11
	7	3	2	3	1	6	4	3	5	10	4
	8	1	1	2	2	2	2	1	3	1	3
	9	3	6	5	6	3	1	6	4	3	3
	10	10	10	14	5	8	7	11	7	5	8
	11	10	8	6	7	4	7	5	3	5	4
	12	10	3	5	5	4	7	6	4	13	5
	13	6	4	6	3	6	7	6	2	5	3
	14	9	9	7	5	8	4	1	5	4	1
	15	5	2	3	4	3	1	3	3	2	3
2	1	17	17	14	16	8	17	20	19	17	15
	2	9	15	8	15	12	4	16	7	11	15
	3	16	13	11	13	11	9	8	13	12	19
	4	14	18	10	18	16	8	11	15	8	17
	5	7	10	5	6	8	11	3	6	1	8
	6	21	16	21	15	17	12	12	16	10	10
	7	8	5	9	12	10	8	9	6	10	10
	8	7	12	9	10	8	7	11	12	12	11
	9	0	1	2	3	4	1	5	2	5	7
	10	8	8	8	8	9	11	11	6	8	13
	11	2	7	6	10	9	8	5	5	0	4
	12	11	8	12	13	11	12	9	15	7	13
	13	10	10	10	12	7	11	8	9	6	7
	14	5	7	5	6	9	7	7	3	6	6
	15	6	10	10	5	3	4	5	7	11	1

progeny with their simulated embryo yield records.

RESULTS

The scaled deviance was 283.5 with 272.5 degrees of freedom, showing no lack of fit. The normal probability plot in figure 1 is almost straight, indicating that the Gamma assumption is plausible. The MAPLE of shape parameter for Gamma distribution was 6.78, which is comparable to the input value 5. Then the variance estimate of the random effects u is $1/6.78 = .15$. The estimates of the underlying means on the log scale were $1.70 \pm .11$ and $2.26 \pm .15$ for the first and second fixed effects, respectively. The results indicated that they correspond to their input values, 1.79 and 2.20.

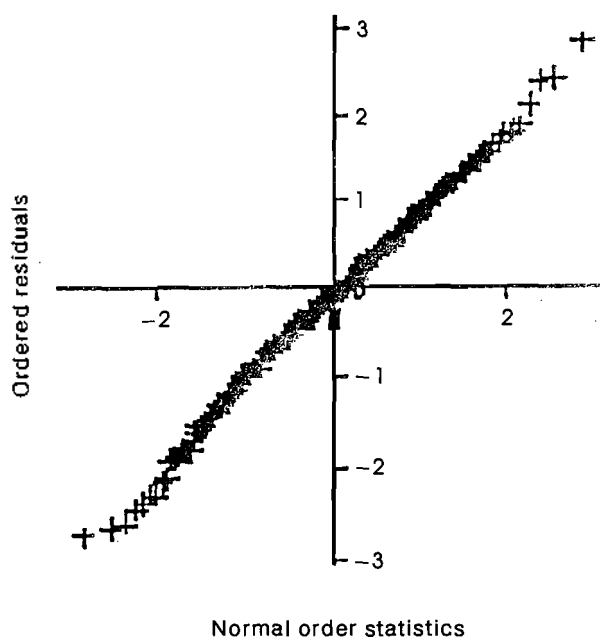


Figure 1. Normal probability plot for residuals of simulated data using a Poisson-Gamma hierarchical generalized linear model.

DISCUSSION

While several researchers (Gianola and Foulley, 1983; Foulley and Gianola, 1984) have suggested the Bayesian estimation of parameters for non-normal data, a hierarchical likelihood-based method derived from a frequentist perspective is utilized in this paper. Subjective decisions on prior distributions of parameters are required in the Bayesian analysis. Generally, the assumption about distributions of β and α can not be verified with any data. In HGLMs, any additional assumptions are not made on these parameters contrary to subjective priors in the

Bayesian analyses.

The random effects are not directly observable, but the assumption on their distributions can be justified by normal probability plot (figure 1). However, with the limited amount of data, a decision ought to be made on the distribution of random effects. When the random components are correlated, the normality assumption is convenient to represent the covariance structure. On the other hand, a merit from the choice of Gamma is that it enables an easy inference on the expected value of observations. With the Poisson GLMM, the expected value of response variate cannot be defined (Foulley and Im, 1993), because $\mu = g^{-1}(\eta) \neq E\{g^{-1}(\eta + v)\} = E(y)$. However, the bias in multiplicative models where $\mu' \mu u$ can be avoided by having a distribution of u satisfying $E(u) = 1$. For example, the first and the second moments for the phenotypes using the Poisson-Gamma HGLM in this study are

$$E(y) = \mu \text{ and}$$

$$\text{var}(y) = E\{\text{var}(y|u)\} + \text{var}\{E(y|u)\} = \mu^2/\alpha + \mu.$$

Therefore, the choice of Gamma leads to an easy inference on the population average. Furthermore, the convergence rate was much faster employing Gamma distribution than employing Normal in several runs with various initial values (Results are not shown). In this study, the use of the conjugate HGLM resulted in fewer numerical problems (e.g. divergence) than the use of Normal density, so that the computational burden is reduced with a conjugate family.

Normality of random effects, which has been assumed by most researchers, may not be always the best choice. In animal breeding, the normality of genetic random effects means the normality of base animals' genetic effects. Most analyses have assumed that base animals are from a complete random population, which is not always the case in reality. Base animals in the population are naturally and artificially selected prior to the generation. As an attempt to reduce this problem, Westell's (1984) genetic groups have been occasionally employed. However, complementary solutions to this approach have not been found to date. In addition, the selection problem could be worse in the less developed countries since they import some superior animals from developed countries. This, in turn, may breach the normality assumption. Although interbull approaches reduce the problem, the use of the method is restricted to the developed countries, e.g. evaluation of conformation trait data from the United States and the Netherlands by Klei (1995). Similar to the case of the normality assumption about base animals, the

normality assumption about the sire of dams effects (or the service sire effects) for embryo yields is practically questionable, because they are unlikely sampled from a random population. Sometimes a flexible density function that allows skewedness may fit those kinds of data better.

A numerator relationship matrix is often employed to explain pedigree in the analyses for animals' genetic merit. With Gamma density used in this study, the covariance structure based on the pedigree is not feasible to construct. To remedy that problem, a Choleski factor can be used; the linear predictor would be $\eta' = X\beta + ZLu$ where L is a lower triangular matrix satisfying $A = LL'$.

Generally, having more than one random components is a concern for analytical models in animal genetic analyses. For example, analytical model for weaning weight evaluation typically includes at least direct genetic, maternal genetic, permanent environmental random effects (Lee and Pollak, 1997). The procedure for the generalization of the hierarchical models is straightforward. Therefore, multiple random effects can be included simultaneously in an analysis with the HGLM. Furthermore, various distributions can be considered for each random effect in HGLMs.

REFERENCES

- Breslow, N. E. and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. *J. Am. Statist. Ass.*, 88, 9-25.
- Everett, R. W. 1996. Personal communication.
- Foulley, J. L. and D. Gianola. 1984. Estimation of genetic merit from bivariate "all-or-none" responses. *Genet. Sel. Evol.* 16:285-306.
- Foulley, J. L., D. Gianola and S. Im. 1987. Genetic evaluation for discrete polygenic traits in animal breeding. In: *Advances in Statistical Methods for Genetic Improvement of Livestock* (Gianola D. and K. Hammond, eds) Springer Verlag, Heidelberg, 361-409.
- Foulley, J. L. and S. Im. 1993. A marginal quasi-likelihood approach to the analysis of Poisson variables with generalized linear mixed models. *Genet. Sel. Evol.* 25, 101-107.
- Gianola, D. and J. L. Foulley. 1983. Sire evaluation for ordered categorical data with a threshold model. *Genet. Sel. Evol.* 15, 201-224.
- Hahn, J. 1992. Attempts to explain and reduce variability of superovulation. *Theriogenology* 38, 269-275.
- Harville, D. A. and R. W. Mee. 1984. A mixed model procedure for analyzing ordered categorical data. *Biometrics* 40, 393-408.
- Hasler, J. F. 1992. Current status and potential of embryo transfer and reproductive technology in dairy cattle. *J. Dairy Sci.* 75, 2857-2779.
- Henderson, C. R. 1975. Best linear unbiased estimation and Prediction under a selection model. *Biometrics*, 31, 423-447.
- Klei, L. 1995. Evaluating Holstein sires for conformation traits using data from the United States and the Netherlands. Ph. D. Dissertation, Cornell University, Ithaca, New York.
- Lee, C. and E. J. Pollak. 1997. Influence of partitioning data by sex on genetic variance and covariance components for weaning weight in beef cattle. *J. Anim. Sci.* 75, 61-67.
- Lee, Y. and J. A. Nelder. 1996. Hierarchical generalized linear models. *J. R. Statist. Soc. B*, 58, 619-678.
- Lohuis, M., C. Smith and E. B. Burnside. 1990. Embryo transfer results in a dispersed nucleus MOET/AI testing scheme. In: *Proc. Fourth World Congress on Genetics Applied to Livestock Production* (W. G. Hill, R. Thompson, J. A. Woolliams, eds) vol. XIV, 221-224.
- Nelder, J. A. and R. W. M. Wedderburn. 1972. Generalized linear models. *J. R. Statist. Soc. A*, 135, 370-384.
- Patterson, H. D. and R. Thompson. 1971. Recovery of interblock information when block sizes are unequal. *Biometrika*, 58, 545-554.
- Perez-Enciso, M., R. J. Tempelman and D. Gianola. 1993. A comparison between linear and Poisson mixed models for litter size in Iberian pigs. *Livest. Prod. Sci.* 35, 303-316.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling and B. P. Flannery. 1992. Numerical recipes in FORTRAN (2nd. ed.). Cambridge Univ. Press, New York.
- Tempelman, R. J. and D. Gianola. 1994. Assessment of a Poisson animal model for embryo yield in a simulated multiple ovulation-embryo transfer scheme. *Genet. Sel. Evol.* 26, 263-290.
- Westell, R. A. 1984. Simultaneous evaluation of sires and cows for a large population. Ph. D. Dissertation. Cornell University, Ithaca, New York.
- Zhao, Y. 1987. Estimation of parameters in a mixed threshold model: its application to dystocia and birth weight in Simmental cattle. Ph. D. Dissertation. Cornell University, Ithaca, New York.