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Genetic evaluation of traits distributed as Poisson-binomial with reference to reproductive characters

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Summary. A procedure of genetic evaluation of reproductive traits such as litter size and survival in a polytocous species under the assumption of polygenic inheritance is described. Conditional distributions of these traits are assumed to be Poisson and Bernoulli, respectively. Using the concept of generalized linear models, logarithmic (litter size) and probit (survival) functions are described as linear combinations of "nuisance" environmental effects and of transmitting abilities of sires or individual breeding values. The liability of survival is expressed conditionally to the logarithm of litter size. Inferences on location parameters are based on the mode of their joint posterior density assuming a prior multivariate normal distribution. A method of estimation of the dispersion parameters is also presented. The use of a "truncated" Poisson distribution is suggested to account for missing records on litter size.

Key words: Genetic evaluation – Reproductive traits – Bayesian methods – Poisson distribution – Threshold characters

Introduction

New methods of genetic evaluation for polygenic discrete traits have been recently developed by Gianola and Foulley (1983), Harville and Mee (1984) and Gilmour et al. (1985).

These methods used the threshold and liability concepts of Wright (1934) for analyzing traits with a (conditional) binomial or multinomial distribution. Extensions to a multiple trait situation, e.g., calving difficulty and survival, have been described by Foulley and Gianola (1984), Höschele et al. (1986) and Foulley et al. (1987), including the case of missing information on some traits (Foulley and Gianola 1986). However, there are situations, at least in animal breeding, in which the data should not be analyzed using such models. First, ordered categorical data are sometimes more suitably described by distributions other than the multinomial. An example is given by the Poisson distribution for counted variates such as ovulation rate or sibship size. Further, when such traits are considered jointly with other discrete characters, the resulting contingency tables show specific patterns which do not fall into the class of incomplete arrays addressed by Foulley and Gianola (1986). For example, if the analysis involves litter size at birth and survival of the young at weaning, there cannot be 2 survivors in a litter of size 1.

The objective of this article is to present a method for joint analysis of Poisson-Binomial data. This would be applicable to polytocous species such as sheep, rabbits, pigs or rodents.

Model

Let 1 and 2 designate traits such as the prolificacy of a female at a given parturition and the survival of young in the litter, respectively. Let y_{1i} be the value of trait 1 in female i ($i = 1, 2, \ldots, n$), and y_{2ij} be the value of trait 2 in young j of female i; the possible outcomes of y_{2ij} are, e.g., dead or alive. Assume as in Im (1982) that given a parameter vector $\boldsymbol{\theta}_1$, the conditional distribution of Y_{1i} is Poisson so:

$$\Pr(Y_{1i} = y_{1i} \mid \boldsymbol{\theta}_1) = \frac{\lambda_i^{y_{1i}} e^{-\lambda_i}}{y_{1i}!}; \quad y_{1i} = 0, 1, \ldots \tag{1}$$

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Above, Y_{1i} is a Poisson random variable having realized value y_{1i}, and λ_i is the Poisson parameter for female i. This parameter, by definition, must be positive. However, the transformation $\eta_i = \ln \lambda_i$, which is the "link" function for Poisson variables (McCullagh and Nelder 1983) can take any value. Hence, it is reasonable to write

$$\eta_i = \mathbf{w}_{1i}' \boldsymbol{\theta}_1 \tag{2}$$

where $\mathbf{w}_{1i}'$ is a known incidence vector and $\boldsymbol{\theta}_1$ contains unknown parameters. The elements of $\boldsymbol{\theta}_1$ are effects of factors affecting the variation of trait 1 such as herd, year, season, parity, age and sire of female.

Let the random vector $\mathbf{Y}_1' = [Y_{11}, Y_{12}, \ldots, Y_{1i}, \ldots, Y_{1n}]$ contain the litter sizes of the females in question, and $\mathbf{Y}_1 = \mathbf{y}_1$ be a particular realization. Given $\mathbf{Y}_1 = \mathbf{y}_1$, the binary variables Y_{2ij} are assumed to follow independent Bernoulli distributions

$$Y_{2ij} \mid \mathbf{y}_1, \boldsymbol{\theta}_1, \boldsymbol{\theta}_2 \sim B(\Pi_{ij}) \tag{3}$$

where Π_{ij} is the conditional probability that young j of litter i survives. It is important to observe that the probability of survival depends on litter size, which is consistent with what is often observed in polytocous species such as the pig. In (3) $\boldsymbol{\theta}_2$ is a vector of parameters affecting the unconditional distribution of Y_{2ij}.

Further, the conditional probability of survival Π_{ij} can be modelled as

$$\Pi_{ij} = \Phi(\mu_{ij}) \tag{4a}$$

where $\Phi(.)$ is the standard normal distribution, and

$$\mu_{ij} = (\tau - \psi_{ij})/\sigma_2 . \tag{4b}$$

In (4b), τ is a threshold value on an underlying (conceptual) normal scale, σ_2 is the residual variance on that scale, which is set conventionally to 1, and ψ_{ij} is a location parameter. If the liability is smaller than τ, young j in litter i survives; death occurs otherwise. Note that μ_{ij} is a parameter of the conditional distribution of Y_{2ij} given $\mathbf{y}_1$, $\boldsymbol{\theta}_1$ and $\boldsymbol{\theta}_2$. By analogy with bivariate regression and setting $\tau = 0$ in (4b), one can write

$$\mu_{ij} = \mathbf{w}_{2ij}' \boldsymbol{\theta}_2 + b(\ln y_{1i} - \eta_i) . \tag{5}$$

From (4b) and (5) it follows that as $\mathbf{w}_{2ij}' \boldsymbol{\theta}_2$ or b increase, so does μ_{ij} and, therefore, the probability of survival Π_{ij}. Note in (5) that given $\boldsymbol{\theta}_2$, $\mathbf{w}_{2ij}' \boldsymbol{\theta}_2$ is the expectation (with minus sign) of an underlying variate which, as in (2), is written as a linear combination of an unknown vector of parameters $\boldsymbol{\theta}_2$ pertaining to the effects of factors affecting variation of trait 2. The second term in (5), similar to that described by Foulley et al. (1983, eq. 19, p 405), takes into account the residual relationship between traits 2 and 1 on the transformed scale. Finally, it should be noted that when $y_{i1} = 0$, (5) does not convey any information on trait 2. This implies that (5) is well defined when a log transformation is used for counts following a Poisson distribution.

Statistical inference

1 Parameterization

Let the entire parameter vector be

$$\boldsymbol{\theta}' = [\boldsymbol{\theta}_1', \boldsymbol{\theta}_2']$$

with $\boldsymbol{\theta}_1' = [\boldsymbol{\beta}_1', \mathbf{u}_1']$ and $\boldsymbol{\theta}_2' = [\boldsymbol{\beta}_2', \mathbf{u}_2']$. The order of $\boldsymbol{\beta}_i$ is $p_i \times 1$ and that of $\mathbf{u}_i$ is $q_i \times 1$ ($i = 1, 2$). Equivalently, we write

$$\boldsymbol{\theta}' = [\boldsymbol{\beta}', \mathbf{u}'] \tag{6}$$

with $\boldsymbol{\beta}' = [\boldsymbol{\beta}_1', \boldsymbol{\beta}_2']$ and $\mathbf{u}' = [\mathbf{u}_1', \mathbf{u}_2']$. The above partition of $\boldsymbol{\theta}$ into $\boldsymbol{\beta}$ and $\mathbf{u}$ is convenient to distinguish parameters on which there is vague prior knowledge ($\boldsymbol{\beta}$), or "fixed" effects in the classical sense (Box and Tiao 1973), from those on which something is known a priori ($\mathbf{u}$), or "random" effects. We assume that $\boldsymbol{\beta}$ and $\mathbf{u}$ are independent a priori so the prior density is

$$p(\boldsymbol{\beta}, \mathbf{u}) = p(\boldsymbol{\beta}) \cdot p(\mathbf{u}) \tag{7a}$$

where $p(\boldsymbol{\beta})$ and $p(\mathbf{u})$ are the marginal densities of $\boldsymbol{\beta}$ and $\mathbf{u}$, respectively. Because $p(\boldsymbol{\beta})$ = constant is an adequate representation of vague prior knowledge for location parameters (Box and Tiao 1973)

$$p(\boldsymbol{\beta}, \mathbf{u}) \propto p(\mathbf{u}) . \tag{7b}$$

Further, arguing from the theory of quantitative inheritance under polygenic control, it is assumed that $\mathbf{u}$ follows the multivariate normal distribution

$$\mathbf{u} \sim N(\mathbf{0}, \boldsymbol{\Sigma}_u) . \tag{7c}$$

A normal prior distribution for parameters has also been employed in probit analysis (e.g., Gianola and Foulley 1983; Foulley et al. 1983) and in log-linear models such as (1) and (2) (Laird 1978; Im 1982).

In animal breeding, the $\mathbf{u}_1$ and $\mathbf{u}_2$ effects can be modelled in different ways depending on the structure of the data and of the matings practiced. For example, if there is one record per female, $\mathbf{u}_1$ could be

$$\mathbf{u}_1' = [a_1^{(1)}, a_2^{(1)}, \ldots, a_i^{(1)}, \ldots, a_n^{(1)}] \tag{8a}$$

or

$$\mathbf{u}_1' = [s_1^{(1)}, s_2^{(1)}, \ldots, s_j^{(1)}, \ldots, s_q^{(1)}] . \tag{8b}$$

In (8a) and (8b) above, $a_i^{(1)}$ is the additive genetic value of female i for trait 1, and $s_j^{(1)}$ is the transmitting ability of sire j for this trait. In the case of (8b), there would be q daughter groups with a certain number of females in each group. Alternatively, the corresponding models with several records per female could be:

$$\mathbf{u}_1' = [a_1^{(1)}, \ldots, a_i^{(1)}, \ldots, a_n^{(1)}, p_1^{(1)}, \ldots, p_i^{(1)}, \ldots, p_n^{(1)}] \quad (9\,a)$$

where $a_i^{(1)}$ is as before and $p_i^{(1)}$ is a permanent environmental effect for female i and trait 1, or

$$\mathbf{u}_1' = [s_1^{(1)}, \ldots, s_j^{(1)}, \ldots, s_q^{(1)}, \quad (9\,b)$$
$$d_{11}^{(1)}, \ldots, d_{1n_1}^{(1)}, \ldots, d_{j1}^{(1)}, \ldots, d_{jn_j}^{(1)}, \ldots, d_{q1}^{(1)}, \ldots, d_{qn_q}^{(1)}]$$

where $s_j^{(1)}$ is as in (8 b) and $d_{jn_j}^{(1)}$ is the effect of daughter n_j of sire j.

Consider next the elements of $\mathbf{u}_2$. As in (8 a), a typical element could be $a_{0,ij}^{(2)} + a_{m,i}^{(2)}$ where $a_{0,ij}^{(2)}$ is the direct additive genetic value of individual i j and $a_{m,i}^{(2)}$ is the maternal additive genetic value of dam i, for trait 2. Letting k be the sire of progeny i j, we have

$$a_{0,ij}^{(2)} = \tfrac{1}{2}[a_{0,i}^{(2)} + a_{0,k}^{(2)}] + \gamma_{ij}$$

where γ_{ij} is a segregation residual with variance $\sigma_{A_0}^2/2$. In a "sire plus maternal grandsire" model, one can define

$$s_{0,k}^{(2)} = \tfrac{1}{2} a_{0,k}^{(2)} \quad (10\,a)$$

$$t_{m,k'}^{(2)} = \tfrac{1}{4} a_{0,k'}^{(2)} + \tfrac{1}{2} a_{m,k'}^{(2)} \quad (10\,b)$$

where k′ is the sire of i. In the model,

$$\sigma_{s_0}^2 = \tfrac{1}{4}\sigma_{A_0}^2$$
$$\sigma_{t_m}^2 = \tfrac{1}{16}\sigma_{A_0}^2 + \tfrac{1}{4}\sigma_{A_m}^2 + \tfrac{1}{4}\sigma_{A_0A_m}$$

and

$$\sigma_{s_0t_m} = (\tfrac{1}{8}\sigma_{A_0}^2 + \tfrac{1}{4}\sigma_{A_0A_m})\, 2\phi_{kk'}$$

where $\phi_{kk'}$ is Malecot's coefficient of coancestry between k and k′. Once the parameterization of $\mathbf{u}_1$ and $\mathbf{u}_2$ is defined, the covariance between $\mathbf{u}_1$ and $\mathbf{u}_2$ can be derived using theory of covariances between relatives including, if necessary, provision for direct and maternal effects (Willham 1963).

2 *Point estimation of genetic merit*

Using Bayes theorem (Box and Tiao 1973) and assuming that b in (5) and $\boldsymbol{\Sigma}_u$ in (7 c) are known, we obtain the posterior distribution of $\boldsymbol{\theta}_1$ and $\boldsymbol{\theta}_2$:

$$p(\boldsymbol{\theta}_1, \boldsymbol{\theta}_2 \mid \mathbf{y}_1, \mathbf{y}_2, b, \boldsymbol{\Sigma}_u)$$
$$\propto p(\mathbf{y}_1, \mathbf{y}_2 \mid \boldsymbol{\theta}_1, \boldsymbol{\theta}_2, b) \cdot p(\boldsymbol{\theta}_1, \boldsymbol{\theta}_2 \mid \boldsymbol{\Sigma}_u) \quad (11\,a)$$
$$\propto p(\mathbf{y}_2 \mid \mathbf{y}_1, \boldsymbol{\theta}_1, \boldsymbol{\theta}_2, b) \cdot p(\mathbf{y}_1 \mid \boldsymbol{\theta}_1) \cdot p(\boldsymbol{\theta}_1, \boldsymbol{\theta}_2 \mid \boldsymbol{\Sigma}_u)$$

because $p(\mathbf{y}_1 \mid \boldsymbol{\theta}_1, \boldsymbol{\theta}_2, b) = p(\mathbf{y}_1 \mid \boldsymbol{\theta}_1)$. Using (7 b), (11 a) can be written as

$$p(\boldsymbol{\theta}_1, \boldsymbol{\theta}_2 \mid \mathbf{y}_1, \mathbf{y}_2, b, \boldsymbol{\Sigma}_u) \quad (11\,b)$$
$$\propto p(\mathbf{y}_2 \mid \mathbf{y}_1, \boldsymbol{\theta}_1, \boldsymbol{\theta}_2, b) \cdot p(\mathbf{y}_1 \mid \boldsymbol{\theta}_1) \cdot p(\mathbf{u} \mid \boldsymbol{\Sigma}_u).$$

From (1), (3), (4 a) and (7 c), the components of (11 b) are:

$$p(\mathbf{u} \mid \boldsymbol{\Sigma}_u) \propto \exp(-\mathbf{u}'\boldsymbol{\Sigma}_u^{-1}\mathbf{u}/2) \quad (12\,a)$$
$$p(\mathbf{y}_1 \mid \boldsymbol{\theta}_1) \propto \prod_i \lambda_i^{y_{1i}} \exp(-\lambda_i)/y_{1i}! \quad (12\,b)$$
$$P(\mathbf{y}_2 \mid \mathbf{y}_1, \boldsymbol{\theta}_1, \boldsymbol{\theta}_2, b) \propto \prod_i \prod_j \Phi[(-1)^{1-y_{2ij}}\mu_{ij}]. \quad (12\,c)$$

Note in (12 c) that if the young survives ($y_{2ij} = 1$), then $\Phi(.)$ is as in (4 a).

The logarithm of the posterior density (11 b) is

$$L(\boldsymbol{\theta}) = \text{constant} + \sum_i \sum_j \ln\{\Phi[(-1)^{1-y_{2ij}}\mu_{ij}]\}$$
$$+ \sum_i (y_{1i}\ln\lambda_i - \lambda_i) - \mathbf{u}'\boldsymbol{\Sigma}_u^{-1}\mathbf{u}/2. \quad (13)$$

It is algebraically convenient to redefine the Poisson variate at the offspring level with

$$y_{1ij} = y_{1ij'}, \quad \eta_{ij} = \eta_{ij'} = \mathbf{w}_{1ij}'\boldsymbol{\theta}_1 \quad (14)$$

which implies that littermates out of female i would have the same Poisson parameter. Using (14), we observe that

$$\sum_j (y_{1i}\ln\lambda_i - \lambda_i) = (y_{1i}\ln\lambda_i - \lambda_i)\, y_{1i}$$

so

$$(y_{1i}\ln\lambda_i - \lambda_i) = \sum_j \frac{(y_{1i}\ln\lambda_i - \lambda_i)}{y_{1i}} = \sum_j \frac{(y_{1ij}\ln\lambda_{ij} - \lambda_{ij})}{y_{1ij}}$$

because $y_{1i} = y_{1ij}$ for all j's, and $\lambda_i = \lambda_{ij}$. However, if $y_{1ij} = 0$, the above expression is not defined but the "contribution" to the posterior density is $e^{-\lambda_{ij}}$, which follows from (1). Hence, the third term in (13) can be written as

$$\sum_i (y_{1i}\ln\lambda_i - \lambda_i) = \sum_i \sum_j \frac{y_{1ij}\ln\lambda_{ij} - \lambda_{ij}}{y_{1ij}^*} \quad (15\,a)$$

where $y_{1ij}^* = 1$ if $y_{1ij} = 0$, and $y_{1ij}^* = y_{1ij}$ otherwise. The second term in (13) needs to be written as

$$\sum_i \sum_j \delta_{1ij} \ln\{\Phi[(-1)^{1-y_{2ij}}\mu_{ij}]\} \quad (15\,b)$$

where $\delta_{1ij} = 0$ if $y_{1ij} = 0$, and 1 otherwise. Using (15 a) and (15 b) in (13), the log-posterior density becomes

$$L(\boldsymbol{\theta}) = \text{constant} + \sum_i \sum_j \left\{ \frac{y_{1ij}\ln\lambda_{ij} - \lambda_{ij}}{y_{1ij}^*} + \delta_{1ij} \right.$$
$$\left. \cdot \ln\Phi[(-1)^{1-y_{2ij}}\mu_{ij}] \right\} - \mathbf{u}'\boldsymbol{\Sigma}_u^{-1}\mathbf{u}/2. \quad (15\,c)$$

The mean of the posterior distribution is an appealing estimator (predictor) of genetic merit because it maximizes expected genetic merit when a fixed number of candidates is to be selected (Bulmer 1980; Goffinet 1983; Goffinet and Elsen 1984; Fernando and Gianola 1986). However, it is difficult to obtain this mean analytically because of nonlinearity so the mode of the posterior distribution is used as a point estimator instead. This mode can be found numerically using, for example, the Newton-Raphson algorithm which requires calculating first and second derivatives of $\mathrm{L}(\boldsymbol{\theta})$ with respect to $\boldsymbol{\theta}$.

Using (2), put now

$$\boldsymbol{\eta} = \begin{bmatrix} \eta_1 \\ \eta_2 \\ \vdots \\ \eta_i \\ \vdots \\ \eta_N \end{bmatrix} = \begin{bmatrix} \mathbf{w}'_{11} \\ \mathbf{w}'_{12} \\ \vdots \\ \mathbf{w}'_{1i} \\ \vdots \\ \mathbf{w}'_{1N} \end{bmatrix} \boldsymbol{\theta}_1 = \mathbf{W}_1 \boldsymbol{\theta}_1 = \mathbf{X}_1 \boldsymbol{\beta}_1 + \mathbf{Z}_1 \mathbf{u}_1 \tag{16}$$

where $\mathbf{X}_1$ and $\mathbf{Z}_1$ are $N \times p_1$ and $N \times q_1$ matrices, respectively; N is now the total number of progeny and $\mathbf{W}_1 = [\mathbf{X}_1, \mathbf{Z}_1]$. Likewise, using (5), put

$$\boldsymbol{\mu}_i = \begin{bmatrix} \mu_1 \\ \mu_2 \\ \vdots \\ \mu_i \\ \vdots \\ \mu_N \end{bmatrix} = \mathbf{X}_2 \boldsymbol{\beta}_2 + \mathbf{Z}_2 \mathbf{u}_2 + b(\dot{\mathbf{y}} - \boldsymbol{\eta}) \tag{17}$$

where $\mathbf{X}_2$ and $\mathbf{Z}_2$ are $N \times p_2$ and $N \times q_2$ matrices, respectively, and $\dot{\mathbf{y}}$ is an $N \times 1$ vector with typical element $\ln(y_{1i})$ $(i = 1, \ldots, N)$. It is clear that (15c) depends on $\boldsymbol{\beta}_i$ and $\mathbf{u}_i$ through λ_{ij}, μ_{ij} and, of course, $\mathbf{u}$. The first derivatives of (15c) with respect to λ_{ij}, η_{ij} and μ_{ij} are

$$\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \lambda_{ij}} = (y_{1ij} - \lambda_{ij})/y^*_{1ij}\,\lambda_{ij} \tag{16a}$$

$$\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \eta_{ij}} = (y_{1ij} - \lambda_{ij})/y^*_{1ij} \tag{16b}$$

$$\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \mu_{ij}} = \delta_{1ij}(-1)^{1-y_{2ij}}\,\phi(\mu_{ij})/\Phi[(-1)^{1-y_{2ij}}\mu_{ij}]. \tag{16c}$$

Then, using the chain-rule through $\boldsymbol{\lambda}_{ij}$, $\boldsymbol{\eta}_{ij}$ and $\boldsymbol{\beta}_1$, we obtain

$$\begin{aligned} \frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \boldsymbol{\beta}_1} &= \sum_i \sum_j \left\{ \frac{(y_{1ij} - \lambda_{ij})}{y^*_{1ij}} \mathbf{x}_{1ij} \right. \\ &\qquad \left. - b \frac{\delta_{1ij}(-1)^{1-y_{2ij}}\phi(\mu_{ij})}{\Phi[(-1)^{1-y_{2ij}}\mu_{ij}]} \mathbf{x}_{1ij} \right\} \\ &= \mathbf{X}'_1 \mathbf{v}_1 \end{aligned} \tag{17a}$$

where $\mathbf{x}_{1ij}$ is the transpose of the appropriate row of $\mathbf{X}_1$, and

$$\mathbf{v}_1 = \left\{ \frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \eta_{ij}} - b \frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \mu_{ij}} \right\}$$

is an $N \times 1$ vector calculated with (16b) and (16c). Similarly

$$\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \boldsymbol{\beta}_2} = \mathbf{X}'_2 \mathbf{v}_2 \tag{17b}$$

where $\mathbf{v}_2 = \left\{ \frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \mu_{ij}} \right\}$ is an $N \times 1$ vector calculated using (16c). In order to calculate the first derivatives with respect to $\mathbf{u}_1$ and $\mathbf{u}_2$, we note in (15c) that

$$\mathbf{u}' \boldsymbol{\Sigma}_u^{-1} \mathbf{u} = [\mathbf{u}'_1 \, \mathbf{u}'_2] \cdot \begin{bmatrix} \boldsymbol{\Sigma}_u^{11} & \boldsymbol{\Sigma}_u^{12} \\ \boldsymbol{\Sigma}_u^{21} & \boldsymbol{\Sigma}_u^{22} \end{bmatrix} \cdot \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix}$$

so it follows directly that

$$\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \mathbf{u}_1} = \mathbf{Z}'_1 \mathbf{v}_1 - \boldsymbol{\Sigma}_u^{11} \mathbf{u}_1 - \boldsymbol{\Sigma}_u^{12} \mathbf{u}_2 \tag{17c}$$

and

$$\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \mathbf{u}_2} = \mathbf{Z}'_2 \mathbf{v}_2 - \boldsymbol{\Sigma}_u^{21} \mathbf{u}_1 - \boldsymbol{\Sigma}_{uu}^{22} \mathbf{u}_2 \,. \tag{17d}$$

Let the log of the posterior density (11b) be written as $\mathrm{L}(\boldsymbol{\theta}) = \mathrm{L}_1(\boldsymbol{\theta}) + \mathrm{L}_0(\boldsymbol{\theta})$ where $\mathrm{L}_1(\boldsymbol{\theta})$ is the log-likelihood and $\mathrm{L}_0(\boldsymbol{\theta})$ is the logarithm of the prior distribution. Then

$$\frac{\partial^2 \mathrm{L}(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}\, \partial \boldsymbol{\theta}'} = \frac{\partial^2 \mathrm{L}_1(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}\, \partial \boldsymbol{\theta}'} + \frac{\partial^2 \mathrm{L}_0(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}\, \partial \boldsymbol{\theta}'} \tag{18a}$$

with

$$\frac{\partial^2 \mathrm{L}_0(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}\, \partial \boldsymbol{\theta}'} = \begin{bmatrix} 0 & 0 \\ 0 & -\boldsymbol{\Sigma}_u^{-1} \end{bmatrix} \tag{18b}$$

and

$$\frac{\partial^2 \mathrm{L}_1(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}_k\, \partial \boldsymbol{\theta}'_l} = -\mathbf{W}'_k \mathbf{R}_{kl} \mathbf{W}_l \quad \begin{matrix} k = 1, 2 \\ l = 1, 2 \end{matrix} . \tag{18c}$$

The $\mathbf{R}_{kl}$ matrices in (18c) are diagonal, of order $N \times N$, having elements:

$$\mathbf{R}_{11} = \{(\lambda_{ij}/y^*_{1ij}) + \delta_{1ij} b^2 v_{2ij}(v_{2ij} + \mu_{ij})\} \tag{19a}$$

where, as before, i j indexes offspring j of female i,

$$\mathbf{R}_{12} = \{-\delta_{1ij}\, b\, v_{2ij}(v_{2ij} + \mu_{ij})\} \tag{19b}$$

and

$$\mathbf{R}_{22} = \{\delta_{1ij}\, v_{2ij}(v_{2ij} + \mu_{ij})\} \,. \tag{19c}$$

The Newton-Raphson algorithm involves iteration with

$$\left[\frac{-\partial^2 \mathrm{L}(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}\, \partial \boldsymbol{\theta}'} \right]_{\boldsymbol{\theta} = \boldsymbol{\theta}^{[t-1]}} (\boldsymbol{\theta}^{[t]} - \boldsymbol{\theta}^{[t-1]}) = \left[\frac{\partial \mathrm{L}(\boldsymbol{\theta})}{\partial \boldsymbol{\theta}} \right]_{\boldsymbol{\theta} = \boldsymbol{\theta}^{[t-1]}} \tag{20}$$

where t is iterate number. Equation (20) can be rearranged as

$$\left[\frac{-\partial^2 L(\boldsymbol{\theta})}{\partial\boldsymbol{\theta}\,\partial\boldsymbol{\theta}}\right]_{\boldsymbol{\theta}=\boldsymbol{\theta}^{[t-1]}} \boldsymbol{\theta}^{[t]} \tag{21}$$

$$= \left[\frac{-\partial^2 L(\boldsymbol{\theta})}{\partial\boldsymbol{\theta}\,\partial\boldsymbol{\theta}'}\right]_{\boldsymbol{\theta}=\boldsymbol{\theta}^{[t-1]}} \boldsymbol{\theta}^{[t-1]} + \left[\frac{\partial L(\boldsymbol{\theta})}{\partial\boldsymbol{\theta}}\right]_{\boldsymbol{\theta}=\boldsymbol{\theta}^{[t-1]}}.$$

Collecting the first derivatives in (17a)–(17d), and the second derivatives in (18a)–(18c), equations (21) can be written as

$$\begin{bmatrix} \mathbf{X}_1' \mathbf{R}_{11} \mathbf{X}_1 & \mathbf{X}_1' \mathbf{R}_{11} \mathbf{Z}_1 & \mathbf{X}_1' \mathbf{R}_{12} \mathbf{X}_2 & \mathbf{X}_1' \mathbf{R}_{12} \mathbf{Z}_2 \\ \mathbf{Z}_1' \mathbf{R}_{11} \mathbf{X}_1 & \mathbf{Z}_1' \mathbf{R}_{11} \mathbf{Z}_1 + \boldsymbol{\Sigma}_u^{11} & \mathbf{Z}_1' \mathbf{R}_{12} \mathbf{X}_2 & \mathbf{Z}_1' \mathbf{R}_{12} \mathbf{Z}_2 + \boldsymbol{\Sigma}_u^{12} \\ \mathbf{X}_2' \mathbf{R}_{21} \mathbf{X}_1 & \mathbf{X}_2' \mathbf{R}_{21} \mathbf{Z}_1 & \mathbf{X}_2' \mathbf{R}_{22} \mathbf{X}_2 & \mathbf{X}_2' \mathbf{R}_{22} \mathbf{Z}_2 \\ \mathbf{Z}_2' \mathbf{R}_{21} \mathbf{X}_1 & \mathbf{Z}_2' \mathbf{R}_{21} \mathbf{Z}_1 + \boldsymbol{\Sigma}_u^{21} & \mathbf{Z}_2' \mathbf{R}_{22} \mathbf{X}_2 & \mathbf{Z}_2' \mathbf{R}_{22} \mathbf{Z}_2 + \boldsymbol{\Sigma}_u^{22} \end{bmatrix}_{\boldsymbol{\theta}=\boldsymbol{\theta}^{[t-1]}} \begin{bmatrix} \boldsymbol{\beta}_1^{[t]} \\ \mathbf{u}_1^{[t]} \\ \boldsymbol{\beta}_2^{[t]} \\ \mathbf{u}_2^{[t]} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1' \mathbf{R}_{11} \bar{\mathbf{y}}_1 + \mathbf{X}_1' \mathbf{R}_{12} \bar{\mathbf{y}}_2 \\ \mathbf{Z}_1' \mathbf{R}_{11} \bar{\mathbf{y}}_1 + \mathbf{Z}_1' \mathbf{R}_{12} \bar{\mathbf{y}}_2 \\ \mathbf{X}_2' \mathbf{R}_{21} \bar{\mathbf{y}}_1 + \mathbf{X}_2' \mathbf{R}_{22} \bar{\mathbf{y}}_2 \\ \mathbf{Z}_2' \mathbf{R}_{21} \bar{\mathbf{y}}_1 + \mathbf{Z}_2' \mathbf{R}_{22} \bar{\mathbf{y}}_2 \end{bmatrix}_{\boldsymbol{\theta}=\boldsymbol{\theta}^{[t-1]}} \tag{22}$$

In (22), the matrices $\mathbf{R}_{kl}$ change values from iterate to iterate, which is clear from (19a)–(19c) and

$$\begin{bmatrix} \bar{\mathbf{y}}_1^{[t]} \\ \bar{\mathbf{y}}_2^{[t]} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 \boldsymbol{\beta}_1^{[t]} + \mathbf{Z}_1 \mathbf{u}_1^{[t]} \\ \mathbf{X}_2 \boldsymbol{\beta}_2^{[t]} + \mathbf{Z}_2 \mathbf{u}_2^{[t]} \end{bmatrix} + \begin{bmatrix} \mathbf{R}_{11}^{[t]} & \mathbf{R}_{12}^{[t]} \\ \mathbf{R}_{21}^{[t]} & \mathbf{R}_{22}^{[t]} \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{v}_1^{[t]} \\ \mathbf{v}_2^{[t]} \end{bmatrix}$$

are "working" variates. Iteration stops when the difference between elements of $\boldsymbol{\theta}^{[t]}$ and $\boldsymbol{\theta}^{[t-1]}$ is deemed sufficiently small. The parallel between (22) and the multiple trait mixed model equations of Henderson and Quaas (1976) should be noted, as observed by Foulley and Gianola (1984) in the context of multivariate binary responses.

"Truncated" Poisson model

Some females do not produce litters after exposure to males or, equivalently, litter size is zero; this is taken into account in the sampling model (1). However, it is sometimes difficult in animal breeding practice to collect such records; in fact, most studies of prolificacy consider data on females that produce at least one offspring. With such data, the sampling model needs to be modified to consider the conditional distribution of litter sizes other than zero. We refer to this as a "truncated" Poisson model, and the probability distribution in (1) becomes:

$$\mathrm{Prob}\,(\mathbf{Y}_{1i} = y_{1i} \mid \boldsymbol{\theta}_1) = \frac{\lambda_i^{y_{1i}}}{y_{1i}!\,(e^{\lambda_i} - 1)}; \quad y_{1i} > 0. \tag{23}$$

If the "truncated" Poisson model is employed, $\mathbf{v}_1$ in (17a) is calculated as before, with

$$\frac{\partial L(\boldsymbol{\theta})}{\partial \eta_{ij}} = \frac{\{y_{1ij} - [\lambda_{ij}/(1 - e^{-\lambda_{ij}})]\}}{y_{1ij}} \tag{24a}$$

and the first term in a typical element of $\mathbf{R}_{11}$ in (19a) replaced by

$$\left(\frac{\lambda_{ij}}{1 - e^{-\lambda_{ij}}}\right)\left(1 - \frac{\lambda_{ij}\, e^{-\lambda_{ij}}}{1 - e^{-\lambda_{ij}}}\right) / y_{1ij}. \tag{24b}$$

Estimation of b and of the components of $\boldsymbol{\Sigma}_u$

The point estimator of $\boldsymbol{\theta}$ described before is the mode of the conditional distribution of $\boldsymbol{\theta}$ given b, $\boldsymbol{\Sigma}_u$ and the data. In many applications, the dispersion matrix has the form $\mathbf{G} \otimes \mathbf{A}$, where $\mathbf{G}$ would be a 2×2 matrix of additive genetic variances and covariances, and $\mathbf{A}$ is a matrix of additive relationships among individuals. Another case is the one where $\mathbf{u}_1$ is a vector of transmitting abilities of sires of females and $\mathbf{u}_2$ contains maternal grandsire effects on the offspring. Here, the elements of $\mathbf{G}$ would be $\sigma_{s_0}^2$, $\sigma_{t_m}^2$ and $\sigma_{s_0 t_m}$ as defined earlier. When b and $\boldsymbol{\Sigma}_u$ are unknown, the problem requires estimating b and $\mathbf{G}$.

In this study we consider a maximum likelihood-type estimator of b. The likelihood function of b is

$$p\,(\mathbf{y}_1, \mathbf{y}_2 \mid \boldsymbol{\theta}, b).$$

It follows from (11b) that information on b stems from

$$p\,(\mathbf{y}_2 \mid \mathbf{y}_1, \boldsymbol{\theta}_1, \boldsymbol{\theta}_2, b)$$

with corresponding log-likelihood L(b). This can be maximized with respect to b using the Newton-Raphson algorithm

$$b^{[t]} = b^{[t-1]} - \left\{\left[\frac{\partial^2 L(b)}{(\partial b)^2}\right]^{-1}\right\} \frac{\partial L(b)}{\partial b} \tag{25a}$$

with

$$\frac{\partial L(b)}{\partial b} = \sum_i \sum_j v_{2ij}\,(\ln y_{1ij} - \eta_{ij}) \tag{25b}$$

and

$$\frac{\partial^2 L(b)}{(\partial b)^2} = -\sum_i \sum_j v_{2ij}\,(v_{2ij} + \mu_{ij})\,(\ln y_{1ij} - \eta_{ij})^2. \tag{25c}$$

The estimation of $\mathbf{G}$ in multivariate threshold models has been discussed in detail by Foulley et al. (1987) and the same approach can be employed here. The procedure estimates $\mathbf{G}$ by maximization of the marginal posterior distribution of the variance and covariance components using a flat prior. Computations involve iteration with

$$\mathbf{G}^{[k+1]} = [(\mathbf{U}'\mathbf{A}^{-1}\,\mathbf{U})^{[k]} + \mathbf{T}^{[k]}]/q \tag{26}$$

where $\mathbf{U}^{[k]} = [\mathbf{u}_1^{[k]}, \mathbf{u}_2^{[k]}]$ is a q × 2 matrix (assume $q_1 = q_2 = q$) with the columns being solutions to (22), conditionally to $\mathbf{G}^{[k]}$ and $b^{[t]}$, and $\mathbf{T}^{[k]}$ is a 2×2 matrix with typical element

$$T_{kl} = \mathrm{tr}(\mathbf{A}^{-1}\mathbf{C}_{kl}) \quad (k = 1, 2,\ l = 1, 2)\,.$$

Above, $\mathbf{C}_{kl}$ is the appropriate $q \times q$ submatrix pertaining to traits k and l of the inverse of the coefficient matrix in (22). It should be noted that the joint estimation of $\boldsymbol{\theta}$, b and $\mathbf{G}$ requires iteration with (22), (25a) and (26) simultaneously. Once the solutions for b and $\mathbf{G}$ converge to $\hat{b}$ and $\hat{\mathbf{G}}$, say, the point estimator of $\boldsymbol{\theta}$ is obtained by solving again (22) with $b = \hat{b}$ and $\mathbf{G} = \hat{\mathbf{G}}$.

The procedure is very general, and it can be applied to models with several sets of random effects. In this case, $\mathbf{u}$ is partitioned into $\mathbf{u}' = [\mathbf{u}'_1, \dots, \mathbf{u}'_l, \dots, \mathbf{u}'_r]$ such that $\boldsymbol{\Sigma}_u$ has the block-diagonal structure

$$\boldsymbol{\Sigma}_u = \bigoplus_{l=1}^{r} \boldsymbol{\Sigma}_{u,l} \tag{27}$$

where $\oplus$ is the direct-sum operator, and

$$\boldsymbol{\Sigma}_{u,l} = \mathbf{G}_l \otimes \mathbf{A}_l\,. \tag{28}$$

Above, $\mathbf{G}_l$ is an $n_l \times n_l$ non-singular matrix of unknown variances and covariances, $\mathbf{A}_l$ is a $g_l \times g_l$ known non-singular matrix, e.g., an identity matrix or a matrix of additive relationships, and $\otimes$ is Kronecker product. The estimator of $\mathbf{G}_l$ has the same form of (26), with appropriate $\mathbf{U}$ and $\mathbf{T}$.

Numerical example

Table 1. Records used in the numerical example

No.	Parity[a]	Sex of lamb[b]	Sire of dam[c]	Y_1[d]	Y_2[e]
1	1	M	1	1	1
2	1	F	1	1	1
3	1	M	1	2	1
4	1	F	1	2	0
5	1	M	1	2	1
6	1	M	1	2	1
7	2	M	1	2	1
8	2	M	1	2	1
9	2	F	2	2	0
10	2	F	2	2	1
11	2	F	2	3	1
12	2	F	2	3	1
13	2	M	2	3	0
14	2	F	2	1	1
15	2	F	2	4	0
16	2	M	2	4	1
17	2	F	2	4	1
18	2	M	2	4	0
19	1	M	3	1	0
20	1	M	3	1	1
21	1	M	3	1	1
22	2	F	3	1	1
23	2	F	3	1	1
24	2	M	3	3	0
25	2	M	3	3	1
26	2	F	3	3	0
27	3	M	3	4	0
28	3	M	3	4	1
29	3	M	3	4	1
30	3	F	3	4	1
31	3	F	3	1	1
32	3	M	3	1	1
33	1	M	4	2	1
34	1	M	4	2	1
35	2	F	4	1	1
36	2	F	4	1	1
37	2	M	4	2	0
38	2	F	4	2	1
39	2	F	4	1	1
40	3	M	4	1	0

[a] Parity of the ewe at parturition
[b] Sex of the young (M: male; F: female)
[c] Sire of the ewe and maternal grandsire of the young
[d] Litter size at birth
[e] Survival (1) and death (0) of the young at weaning

A small hypothetical data set was employed to illustrate the procedures. The data (Table 1) consist of records on litter size of 24 ewes, and survival records at weaning on their 40 lambs. The model for the linear predictor (2) associated with the Poisson parameter for litter size was:

$$\eta_{mn} = P_m + s_n$$

where P_m is an effect of parity of dam ($m = 1,2,3$) and s_n is the transmitting ability of the sire of the ewe ($n = 1, \dots, 4$). The "truncated" Poisson model was used in the calculations. The model for the location parameter (5) in the underlying survival liability scale was

$$\mu_{mnop} = P^*_m + A_n + t_o + b\,(\ln y_{1mnop} - \eta_{mn})\,.$$

where P^*_m is the effect of parity of dam, A_n is the effect of sex of lamb ($n = 1, 2$ for males and females, respectively), t_o is the effect of the maternal grandsire ($o = 1, \dots, 4$) and b is the residual regression of liability of survival on the log of litter size. The parameter vector consists of

$$\boldsymbol{\beta}' = [P_1, P_2, P_3, P^*_1, P^*_2, P^*_3, A_1, A_2]\,,$$

$$\mathbf{u}' = [s_1, s_2 \dots, s_4, t_1, t_2 \dots, t_4]$$

and the residual regression b was also estimated. Prior knowledge on $\boldsymbol{\beta}$ was assumed vague. As in (7c), $\mathbf{u}$ was assumed multivariate normal with dispersion matrix

$$\mathrm{Var}(\mathbf{u}) = \mathbf{G} \otimes \mathbf{I}_4$$

where

$$\mathbf{G} = \begin{bmatrix} \sigma_s^2 & \sigma_{st} \\ \sigma_{st} & \sigma_t^2 \end{bmatrix}$$

with σ_s^2 and σ_t^2 are the variances among sire of dam effects for litter size and survival, respectively, and σ_{st} their covariance. Parameters values of $\sigma_s^2 = 1/25.667$, $\sigma_t^2 = 1/15$ and $\sigma_{st} = -0.25\,\sigma_s\,\sigma_t$ were used in the calculations. The value of σ_s^2 corresponds to a "heritability" coefficient on the η scale of 0.244 which is equal to $4\sigma_s^2/(\sigma_s^2 + \lambda^{-1})$, with $\lambda = 5/3$ being the "average" Poisson parameter. Note that the residual variance is approximately λ^{-1}, which can be obtained from a first order Taylor series expansion of η. The value for σ_t^2 corresponds to a heritability of survival in the probit scale of 1/4, and a genetic

Table 2. Estimates of parameters and of their posterior precision [a]

Litter size (Y_1)		Survival (Y_2)	
Parameter	Estimate	Parameter	Estimate
P_1	-0.3880 ± 0.5647	$P_1^* + A_1$	1.2367 ± 0.5648
P_2	-0.3135 ± 0.3110	$P_2^* + A_1$	0.5466 ± 0.4562
P_3	0.2659 ± 0.5566	$P_3^* + A_1$	0.8135 ± 0.6323
		$A_2 - A_1$	0.3656 ± 0.4809
s_1	0.0324 ± 0.1908	t_1	0.0606 ± 0.2441
s_2	0.0842 ± 0.1876	t_2	-0.0685 ± 0.2408
s_3	-0.0324 ± 0.1851	t_3	-0.0009 ± 0.2364
s_4	-0.0842 ± 0.1855	t_4	0.0088 ± 0.2390

[a] From the inverse of the coefficient matrix in equation (22), evaluated after convergence

Table 3. Estimates of marginal probabilities in parity 3, by sire

Sire	Survival [a]	Litter size						
		1	2	3	4	5	6	7
1	0.851	0.473	0.319	0.143	0.048	0.013	0.003	0.001
2	0.819	0.453	0.321	0.152	0.054	0.015	0.004	0.001
3	0.836	0.498	0.315	0.132	0.042	0.011	0.002	0.000
4	0.839	0.517	0.310	0.124	0.037	0.009	0.002	0.000

[a] Averaged over sex of lamb

correlation of -0.25 between litter size and survival was assumed to obtain σ_{s1}.

The unknown parameters were estimated iterating with equations (22) and (25a). The solution for $\hat{b}$ was $b = -0.5575 \pm 0.2819$ irrespective of the starting value used ($b_0 = -2$, 0 or 1.5). From (5), a negative estimate would imply that the probability of survival is smaller in larger litters. The solutions for the elements of $\boldsymbol{\theta}$ are in Table 2. A discussion of the results will not be given because the data set is entirely hypothetical; the objective of the example was to provide a numerical illustration of the procedure. Fifty rounds of iteration with (22) and (25a) were required to reach "convergence". In trials where b was set to a fixed value, only 5 rounds were required to satisfy the stopping rule

$$\left\{\sum_i [\theta_i^{[t+1]} - \theta_i^{[t]}]^2/16\right\}^{1/2} \leqq 10^{-8}.$$

Estimates of marginal probabilities of survival, and of litter size falling in a particular class were obtained as suggested by Gianola and Foulley (1983), Foulley et al. (1983) and Foulley and Gianola (1984). The estimates for litter size presented in Table 3 can be interpreted as the probability distribution of an infinite number of third parity daughters of the appropriate sire; the data suggest that litters larger than 4 would be extremely unlikely in the population in question. The same was done for survival, and the marginal probabilities presented are averages of probabilities obtained separately for each sex of lamb.

Discussion

This paper is a contribution to the development of procedures for genetic analysis of traits that do not follow the normal distribution. In particular, methods are described for the situation where the Poisson and Bernoulli distributions provide reasonable models for describing traits related to fitness such as litter size and post-natal survival in a polytocous species. Emphasis was on a model for joint analysis of litter size and survival, as it is known that the probability of perinatal or pre-weaning survival depends on litter size.

Following McCullagh and Nelder (1983), logarithms of Poisson parameters for litter size were modeled as linear functions of explanatory variables. Likewise, the probit of the probability of survival, the trait viewed as a Bernoulli variate, was expressed as a linear model. Survival was related to litter size via the linear residual regression of the probit on the logarithm of litter size; perhaps other alternatives may be employed to describe such relationship. A plot of survival against litter size may suggest a suitable relationship. "Random" effects were introduced in the model via a Bayesian treatment as suggested by Im (1982) for Poisson variables, and by Gianola and Foulley (1983) and Foulley and Gianola (1984) for threshold characters. The incorporation of random effects constitutes an additional level of generalization of the theory of generalized linear models.

In this paper, residual variation in the model for litter size was accounted for using a Poisson distribution with parameter $\lambda_k = \exp(\mathbf{w}'_{1k}\boldsymbol{\theta}_1)$, which in fact is the conditional distribution of litter size given θ_1. This model is flexible enough to accommodate situations encountered in animal breeding such as repeated records so that the linear model can include additive genetic and permanent environmental effects. Here, the residual variance would be Poisson with a parameter peculiar to each female. A somewhat similar approach was employed for growth curve parameters by Kachman (1985), who modelled variation about the growth curve of each individual with a multivariate normal distribution allowing, if needed, autocorrelation among the residuals. Sometimes, due to biological constraints, litter size cannot exceed a certain value. In this case it would be more appropriate to consider a Poisson model truncated both on the "left" and on the "right".

Implementation of the procedure requires solving the nonlinear system in (22). Some simplifications can be made when the columns of $\mathbf{X}_1$ and $\mathbf{Z}_1$ are subsets of columns of $\mathbf{X}_2$ and $\mathbf{Z}_2$, respectively, i.e., when $\mathbf{X}_1 = \mathbf{X}_2 P$ and $\mathbf{Z}_1 = \mathbf{Z}_2\mathbf{Q}$. Letting $\tilde{\boldsymbol{\beta}}_2 = \boldsymbol{\beta}_2 - b\,\mathbf{P}\,\boldsymbol{\beta}_1$ and $\tilde{\mathbf{u}}_2 = \mathbf{u}_2 - b\,\mathbf{Q}\,\mathbf{u}_1$, $\boldsymbol{\mu}_{ij}$ in (5) can be written as $\boldsymbol{\mu}_{ij} = \mathbf{x}'_{2ij}\tilde{\boldsymbol{\beta}}_2 + \mathbf{z}'_{2ij}\,\tilde{\mathbf{u}}_2 + \ln(y_{1ij})$. This is the reparameterization given in Foulley et al. (1983) for the prediction of genetic merit with a mixture of binary and quantitative traits. The resulting system in $\boldsymbol{\beta}_1$, $\mathbf{u}_1$, $\boldsymbol{\beta}_2$, $\mathbf{u}_2$ has the same form of (22) with the following modifications:

$$\tilde{\mathbf{R}}_{11} = \{\lambda_{ij}/y^*_{1ij}\}\,; \quad \tilde{\mathbf{R}}_{12} = \mathbf{0}\,; \quad \tilde{\mathbf{R}}_{22} = \{\delta_{1ij}\,\tilde{v}_{2ij}(\tilde{v}_{2ij} + \mu_{ij})\}$$

$$\tilde{\mathbf{y}}_i = \mathbf{X}_i \tilde{\boldsymbol{\beta}}_i + \mathbf{Z}_i \tilde{\mathbf{u}}_i + \tilde{\mathbf{R}}_{ii}^{-1} \tilde{\mathbf{v}}_i \quad \text{for} \quad i = 1, 2$$

$$\tilde{\mathbf{v}}_1 = \{(y_{1ij} - \lambda_{ij})/y^*_{1ij}\}\,; \quad \tilde{\mathbf{v}}_2 \text{ as in (16c)}.$$

In addition, the blocks in the inverse of $\boldsymbol{\Sigma}_u$ are now calculated from

$$\tilde{\boldsymbol{\Sigma}}_u = \begin{bmatrix} \mathbf{I} & \mathbf{0} \\ -b\,\mathbf{Q} & \mathbf{I} \end{bmatrix} \cdot \boldsymbol{\Sigma}_u \cdot \begin{bmatrix} \mathbf{I} & -b\,\mathbf{Q} \\ \mathbf{0} & \mathbf{I} \end{bmatrix}.$$

The procedure requires knowing the residual regression coefficient b and the variance-covariance matrix of the random effects u. When these are unknown, a method was described to estimate these parameters along the lines of Gianola et al. (1986) in the normal distribution, and Foulley et al. (1987) in the analysis of polygenic binary traits. In general, this leads to empirical Bayes estimators of $\boldsymbol{\beta}$ and $\mathbf{u}$.

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