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Fitting different nonlinear mixed models to the egg laying records

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Introduction

In modern poultry breeding, the selection for egg production has pushed the performance of commercial layers close to their biological and parametric limits. As total egg number approaches these limits, phenotypic and genetic variation in traditional measures decreases, making further genetic progress difficult (Bain *et al*., 2016). To address this issue, the industry is exploring extended laying cycles, with production periods reaching up to 100 weeks without induced molting (Molnar *et al*., 2016). From a quantitative genetics' perspective, a key challenge of these extended cycles is the statistical properties of egg production data.

Standard procedures for estimating genetic variance components and predicting breeding values have traditionally relied on linear mixed models assuming a Gaussian distribution (Henderson, 1973). However, egg production records are discrete outcomes defined over a fixed number of days and typically show a highly skewed distribution, with most hens laying eggs on most days and relatively few non-laying events. This concentration near the upper bound is not well captured by the assumption of a Gaussian distribution, as this does not naturally reflect the discreteness or asymmetry of the data. Generalized linear mixed models (GLMM) provide a flexible framework that allows the use of nonlinear distributions to better adjust the statistical properties of traits (Tempelman, 1998). An alternative parameterization is to define the trait as the number of days without egg production, thereby shifting the focus to relatively rare events and making the trait more suitable for modeling with count distributions such as the Poisson. Furthermore, egg data may also exhibit overdispersion, where the variance exceeds the mean expected under a Poisson model, justifying the use of other distributions such as the Negative Binomial or Multiplicative Binomial.

Therefore, the objective of this study was to evaluate whether nonlinear GLMM could offer an alternative to the traditional Gaussian approach for analyzing egg records in laying hens.

Materials & Methods

Data description and trait definition. The dataset consisted of egg laying records from one high-performing purebred White Leghorn line from the genetic breeding program of the Lohmann Breeders Company. Hens not surviving until the end of the production cycle were excluded. After filtering, the dataset included 8,030 hens, with 335 males in the pedigree. Egg production was recorded over 20 consecutive 28-day periods, covering the age interval from 20 to 100 weeks. The analyzed trait was the egg yield gap (EYG), defined as the difference between the maximum possible production within each period (28 eggs) and the number of eggs laid. This makes the EYG a discrete count ranging from 0 to 28. The mean (standard deviation) of the EYG was 1.30 (1.88) in this population.

Statistical models. GLMMs were used to relate the EYG to fixed and random effects through an appropriate link function, ensuring that predictions remained within the valid range implied by each distribution. The linear predictor included a fixed effect of laying period and two random effects: the additive genetic effect (**a**) and the permanent environmental effect (**p**). The following distributions were evaluated: 1) The classical approach, based on the assumption of normality (NM). 2) Poisson (PM), with a log link, assuming equality between the mean and variance. 3) Binomial (BM), modeling the count as successes out of 28 trials, using a logit link. 4) Negative binomial (NBM), extending the PM by including an overdispersion parameter (ω). A log link function was used, as in the PM. 5) Multiplicative binomial (MBM), a flexible extension of the binomial distribution that includes an additional dispersion parameter (ϕ) to account for dependence among trials. A logit link function was used as in BM to model the probability of laying daily.

Bayesian inference and MCMC implementation. All models were fitted within a Bayesian hierarchical framework. Flat priors were assigned to systematic effects, variance components, and dispersion parameters. Additive genetic effects were assumed to follow a multivariate normal distribution, such that $\mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma^2_a)$, where **A** is the numerator relationship matrix derived and σ^2_a is the additive genetic variance. Permanent environmental effects were assumed as $\mathbf{p} \sim N(\mathbf{0}, \mathbf{I}\sigma^2_p)$, where **I** is the identity matrix and σ^2_p is the permanent environmental variance. Posterior distributions were obtained using Markov Chain Monte Carlo (MCMC) methods. For the NM, all parameters were updated using Gibbs sampling. For the nonlinear GLMM, variance components were sampled via Gibbs Sampling, while the remaining parameters were updated using single-site Metropolis–Hastings random-walk proposals due to the lack of closed-form full conditionals (Chib and Greenberg, 1995). MCMC chains were run for 500,000 iterations to ensure adequate mixing, with the first 100,000 discarded as burn-in. The MCMC implementation was carried out using a custom Fortran programme for the GLMM, whereas BLUPF90+ was used for the classical approach. Convergence was assessed by visual inspection of trace plots for all variance components and dispersion parameters.

Model comparison and predictive ability. Model fit between nonlinear GLMM was compared using two simple criteria: 1) Deviance Information Criterion (DIC), which measures the overall quality of the model while penalizing excessive complexity, with lower values indicating better performance. A difference of 7 DIC units is commonly considered sufficient to favor one model over another (Spiegelhalter *et al*., 2002). Previous studies have shown that more complex models may be preferred when they achieve a substantial reduction in DIC (Sae-Lim *et al*., 2017; Varona *et al*., 2020). 2) log-marginal probability (logCPO): Evaluates the model's ability to predict each phenotypic observation, with higher values indicating superior predictive performance. DIC and logCPO were not computed for the NM because these criteria are only comparable across models that share the same likelihood structure. In contrast, genetic predictive ability and selection decisions were evaluated across all models: predictive ability was assessed using the LR method for the last generation (Legarra and Reverter, 2018), and selection consistency was measured as the percentage of overlap in the top 10% and 30% ranked individuals.

Estimation of heritability. Heritability (h^2) was estimated from the posterior samples of the variance components. After burn-in, h^2 was computed at each MCMC iteration as the ratio of additive genetic variance to total phenotypic variance, and posterior means and 95% highest posterior density (HPD95) intervals were derived. The residual variance was defined by the assumed response distribution (Foulley *et al*., 1992): in NM, it was obtained directly from the posterior variance components; in PM, it depended on the estimated mean, in BM, on the

number of trials and the estimated success probability, in NBM, it additionally accounted for overdispersion; and in MBM, it was further adjusted to reflect correlation among trials within individuals. h^2 was also expressed on the observed data scale using posterior predictions and a log-normal correction to facilitate biological interpretation and comparison across models.

Results & Discussion

Model comparison and goodness of fit. The NBM performed best overall, consistent with the empirical characteristics of the data, in which the variance exceeded the mean. The NBM provided a more robust framework in these scenarios, as they include a specific dispersion parameter to absorb extra-Poisson variation (Tempelman and Gianola, 1996).

Table 1. Goodness of fit and model comparison criteria.

Model	DIC[1]	logCPO[2]
Poisson (PM)	470,591.2	-240,539.4
Binomial (BM)	511,666.9	-263,074.3
Negative Binomial (NBM)	**432,096.3**	**-217,461.9**
Multiplicative Binomial (MBM)	499,130.1	-261,437.5

[1]Deviance Information Criteria
[2]log-marginal probability

The PM showed the poorest fit. While the BM reflects the discrete nature of daily laying, its lower fit suggests that assuming independent Bernoulli trials fails to account for the biological dependence and increased variability typical of extended cycles (Varona and Sorensen, 2010). Although the MBM incorporates extra-binomial variation through trial correlation, its performance remained inferior to the NBM. This indicates that modeling overdispersion as a continuous mixture at the count level provides the necessary flexibility to capture the highly overdispersed nature of the egg record (Sae-Lim *et al*., 2017).

Genetic parameters and heritability estimates. Approximated observed scale h^2 estimates were low but remarkably stable across the different response distributions, ranging from 0.046 (NM) to 0.064 (MBM) (Table 2). This consistency indicates that the proportion of phenotypic variance attributable to additive genetic effects is robust to the choice of link function and distribution, despite differences in how residual variation is modeled.
This indicates that EYG is largely influenced by environmental and physiological factors, as expected for reproductive traits. The inclusion of a permanent environmental effect was important to account for persistent individual-specific influences across the 20 laying periods, preventing inflation of additive genetic variance. Although a repeatability model was used, the heritability of reproductive traits is known to vary across repeated laying periods (Bain *et al*., 2016). In this context, EYG showed consistent and estimable genetic parameters under all modelling approaches, supporting its use in genetic evaluations under extended production conditions (Arunalthan *et al*., 2024).

Table 2. Observed scale heritability estimates (Posterior Mean and HPD95)

Model	Posterior Mean	HPD95[1]
Normal (NM)	0.046	0.037 - 0.056
Poisson (PM)	0.058	0.052 - 0.065
Binomial (BM)	0.064	0.059 - 0.073
Negative Binomial (NBM)	0.056	0.051 - 0.066
Multiplicative Binomial (MBM)	0.064	0.059 - 0.074

[1]95% Higher Posterior Density

Overdispersion estimates. The NBM showed marked overdispersion (ω = 2.50; HPD95: 2.49–2.51), confirming a strong departure from the Poisson assumption. In contrast, the MBM produced a dispersion parameter very close to 1 (ϕ = 0.998; HPD95: 0.998–0.999), indicating minimal within-individual correlation among trials. These results suggest that the extra variability present in the data is better captured at the aggregated count level, which explains the superior performance of the NBM. Adjusting for this dispersion could lead to more reliable parameter estimates.

Predictive ability. The NM showed the lowest predictive accuracy (0.192), whereas all nonlinear GLMMs yielded higher and similar values, ranging from 0.259 (MBM) to 0.275 (PM and NBM). This result suggests that accounting for the discrete nature of the trait improves predictive performance.
Rankings were also more consistent among the nonlinear GLMMs: agreement ranged from 93–98% for the top 30% and from 88–98% for the top 10%. In contrast, concordance between the GLMMs and the NM was notably lower (82–85% for the top 30% and 72–79% for the top 10%), indicating that model choice may affect selection decisions.

Conclusions

The results show that using nonlinear GLMM could provide a clearer representation of the statistical properties of egg records than a classical approach. Among the evaluated distributions, the NBM offered the best fit to the data by accommodating the substantial overdispersion observed. Cross-validation further indicated that the nonlinear GLMM achieved higher predictive ability than the NM. Ranking comparisons also revealed strong agreement among the alternative GLMM, while their concordance with the Gaussian approach was notably lower, especially when focusing on the top-ranked individuals. Overall, these findings support the use of nonlinear GLMM as a suitable alternative framework for analysing egg counts in genetic evaluations of laying hens.

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