

## Article

# When Is Poisson Enough? A Likelihood-Based Comparison of Poisson and Negative Binomial GLMMs for Owl Nestling Call Counts

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## Abstract

Modeling count data using generalized linear mixed models (GLMMs) is a common practice in ecological research. However, datasets such as bird vocalization counts often display overdispersion, where the variance exceeds the mean, violating Poisson assumptions and potentially leading to biased inference. This study investigates the call counts of owl nestlings by comparing Poisson and Negative Binomial (NB) GLMMs to assess the impact of overdispersion on model performance. The models incorporate a random intercept for nest identity, thereby accounting for the hierarchical structure of the data and the correlation among observations within the same nest. Parameter estimation was performed using the Laplace approximation and the Adaptive Gauss–Hermite Quadrature (AGHQ) method to evaluate likelihood-based inference under different estimation approaches. Although the overdispersion diagnostic indicated extra-Poisson variation, model comparison based on the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and log-likelihood showed that the Poisson GLMM provided a better overall fit than the NB-GLMM. These findings demonstrate that the presence of overdispersion alone does not necessarily justify replacing a Poisson GLMM with a NB-GLMM and highlight the importance of combining distributional diagnostics with likelihood-based model selection when analyzing hierarchical ecological count data.

**Keywords:** generalized linear mixed models (GLMMs); overdispersion; owl nestlings; adaptive gaussian hermite quadrature (AGHQ); Laplace approximation

**MSC:** 62J12; 62P12; 62F99



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## 1. Introduction

Statistical models for count data have become fundamental in ecological and behavioral research, particularly in ornithological studies where response variables such as call counts, feeding rates, or movement frequencies are discrete, non-negative integers. Traditionally, these data were often analyzed using generalized linear models (GLMs) with the Poisson distribution as a canonical choice due to its simplicity and direct interpretation [1]. However, one major limitation of the Poisson model is its restrictive assumption of equidispersion, where the mean equals the variance. In real-world ecological contexts, count data often display overdispersion, meaning the variance exceeds the mean due to unobserved heterogeneity, behavioral variability, or environmental noise [2,3]. Ignoring this feature can lead to underestimated standard errors, inflated type I error rates, and ultimately unreliable inference [4].

To address this issue, the negative binomial (NB) distribution has been proposed as a flexible alternative to the Poisson, as it incorporates an additional dispersion parameter to capture variance beyond that explained by the mean alone [5,6]. When combined with random effects to account for nested data structures, this leads to the negative binomial generalized linear mixed model (NB-GLMM)—a powerful framework for analyzing overdispersed count data in hierarchical ecological settings. The random effects capture unmeasured variability at different levels (e.g., individual, nest, or observation session), while the NB distribution accounts for residual overdispersion. This dual flexibility is especially important in behavioral ecology, where response variability can arise from both structured and unstructured sources.

Fitting such models, however, presents computational challenges. Unlike GLMs, whose parameters are typically estimated using iterative likelihood-based algorithms, GLMMs involve random effects that require numerical integration because their marginal likelihoods do not have closed-form solutions. Consequently, approximate integration methods are required for parameter estimation. The most accurate and increasingly popular techniques are the Laplace approximation and the Adaptive Gaussian-Hermite Quadrature (AGHQ) method [7–9]. Unlike simpler techniques such as penalized quasi-likelihood or Laplace approximation [10], AGHQ dynamically adjusts quadrature nodes to better approximate the posterior distribution of random effects. Studies have demonstrated that AGHQ yields more accurate estimates of fixed effects, variance components, and standard errors, especially in models with small to moderate sample sizes and complex random effect structures [10,11]. The application of GLMMs combined with sophisticated estimation techniques such as Laplace approximation and AGHQ enables researchers to explore complex ecological dynamics, especially in avian research, where behavioral responses and environmental factors frequently exhibit nonlinear relationships and hierarchical structures.

In practical applications within R, AGHQ can be implemented using the `glmer()` function from the `lme4` package by specifying the number of quadrature nodes (`nAGQ`) greater than one [12]. The `glmer()` function supports up to 25 adaptive nodes when the default Nelder-Mead optimizer is employed, offering researchers flexibility in balancing computational cost and estimation fidelity [13]. This approach is applicable specifically to Poisson and binomial GLMMs, allowing direct control over the precision of the approximation. In contrast, NB-GLMMs can be implemented using the `glmmTMB()` function from the `glmmTMB` package by specifying the appropriate family (`nbinom1` or `nbinom2`). Unlike `glmer()`, `glmmTMB()` does not allow manual specification of the number of adaptive quadrature nodes, but it uses a Laplace approximation by default, providing a reliable balance between computational efficiency and estimation accuracy. Therefore, while Poisson GLMMs offer explicit control over AGHQ parameters, NB-GLMMs rely on the default Laplace approximation for estimation.

In the field of avian behavioral ecology, GLMMs have become indispensable for exploring the effects of parental care and environmental conditions on offspring behavior. For example, Roulin et al. [14,15] investigated vocal begging behavior in barn owl (*Tyto alba*) nestlings and found that chicks beg more intensely in the presence of their mother than their father. Their findings suggest a form of parent-specific signaling potentially shaped by differential parental investment. While that study focused solely on parental presence, it opened the door to further exploration of other ecological covariates, such as brood size and food availability. Building upon this, Rich [12] analyzed similar ecological datasets using simulation-based approaches to evaluate the performance of various GLMM estimation techniques, including Laplace and AGHQ, under conditions of overdispersion and multiple random effects. Their work emphasized the critical role of method selection in deriving reliable ecological inferences.

In light of this background, our study revisits the owl nestling call count dataset originally used by Roulin et al. [14,15] and expanded by Rich [12], aiming to re-analyze these data using both a Poisson GLMM estimated via glmer with AGHQ and a NB-GLMM estimated via glmmTMB with Laplace approximation. Unlike earlier approaches, we explicitly account for the hierarchical structure of the data through a random intercept for nest identity and compare Poisson and Negative Binomial GLMMs under commonly used estimation approaches. We focus on three key predictors: brood size, food treatment, and parental arrival identity. More importantly, this study investigates whether the presence of overdispersion alone is sufficient to justify replacing a Poisson GLMM with a NB-GLMM, or whether likelihood-based model selection criteria may still favor the simpler Poisson specification.

The remainder of the paper is organized as follows: Section 2 introduces the theoretical background of NB-GLMMs, Laplace and AGHQ estimation. Section 3 outlines the data, variables, and modeling strategy. Section 4 presents the results. Finally, Section 5 concludes with a reflection on the advantages of using Laplace and AGHQ in small-scale ecological studies and provides directions for future research.

## 2. Theoretical Background

GLMMs have become a cornerstone of modern statistical modeling in ecology, particularly when data exhibit both non-normal response distributions and hierarchical structure [11,16]. For count data, the canonical model is the Poisson GLMM, which assumes that the conditional mean of the response variable equals its variance and follows a log link function. However, ecological and behavioral datasets often show substantial overdispersion, a condition where the variance exceeds the mean due to latent heterogeneity, stochastic processes, or unobserved covariates [2,4]. In such cases, reliance on the Poisson distribution leads to biased parameter estimates and invalid statistical inferences [3].

For the Poisson GLMM, the conditional distribution of the response variable is given by  $Y_{ij}|b_i \sim \text{Poisson}(\mu_{ij})$  where  $Y_{ij}$  denotes the observed count for observation  $j$  within cluster  $i$ ,  $b_i$  denotes the random intercept for cluster  $i$ , and  $\mu_{ij}$  is the conditional mean. The conditional probability mass function is  $P(Y_{ij} = y_{ij}|b_i) = \frac{\mu_{ij}^{y_{ij}} \exp(-\mu_{ij})}{y_{ij}!}$ ,  $y_{ij} = 0, 1, 2, \dots$ . The conditional expectation and variance satisfy  $E(Y_{ij}|b_i) = \mu_{ij}$ ,  $\text{Var}(Y_{ij}|b_i) = \mu_{ij}$ .

A logarithmic link function is employed to relate the conditional mean to the linear predictor,  $\log(\mu_{ij}) = \eta_{ij} = x_{ij}^T \beta + z_{ij}^T b$ , where  $x_{ij}$  denotes the vector of fixed-effect covariates,  $\beta$  is the corresponding vector of regression coefficients,  $z_{ij}$  is the random-effects design vector, which yields the exponential mean function  $\mu_{ij} = \exp(x_{ij}^T \beta + z_{ij}^T b)$ . The random effects are assumed to follow a normal distribution,  $b_i \sim N(0, \sigma_b^2)$ , thereby accounting for the correlation among observations within the same cluster.

To account for overdispersion, the NB distribution is frequently used as a more flexible alternative. Originating from the Poisson–Gamma mixture model [5], the conditional distribution is given by  $Y_{ij}|b_i \sim \text{NB}(\mu_{ij}, \theta)$ , where  $\theta > 0$  denotes the dispersion parameter controlling the degree of overdispersion. The conditional probability mass function is  $P(Y_{ij} = y_{ij}|b_i) = \frac{\Gamma(y_{ij} + \theta)}{\Gamma(\theta) y_{ij}!} \left( \frac{\theta}{\theta + \mu_{ij}} \right)^\theta \left( \frac{\mu_{ij}}{\theta + \mu_{ij}} \right)^{y_{ij}}$ ,  $y_{ij} = 0, 1, 2, \dots$ . The conditional expectation and variance are  $E(Y_{ij}|b_i) = \mu_{ij}$ ,  $\text{Var}(Y_{ij}|b_i) = \mu_{ij} + \frac{\mu_{ij}^2}{\theta}$ , corresponding to the nbinom2 parameterization implemented in the glmmTMB package in R.

As in the Poisson GLMM, the logarithmic link function relates the conditional mean to the linear predictor,  $\log(\mu_{ij}) = \eta_{ij} = x_{ij}^T \beta + z_{ij}^T b$ , which implies the exponential mean function  $\mu_{ij} = \exp(x_{ij}^T \beta + z_{ij}^T b)$ .

The complete NB-GLMM is therefore specified as  $Y_{ij}|b_i \sim NB(\mu_{ij}, \theta)$ ,  $\log(\mu_{ij}) = \eta_{ij} = x_{ij}^T\beta + z_{ij}^Tb$ ,  $b_i \sim N(0, \sigma_b^2)$ . The model parameters, including the fixed effects, random-effects variance components, and the dispersion parameter, are estimated by maximizing the marginal likelihood. Since the marginal likelihood has no closed-form solution, numerical integration based on the Laplace approximation is employed, as implemented in the glmmTMB package.

This adjustment is particularly effective in behavioral studies where count responses are influenced by both fixed predictors and idiosyncratic factors such as individual variation or environmental conditions. When combined with random effects to accommodate hierarchical data structures, NB-GLMM emerges as a robust modeling framework. The random effects component in NB-GLMMs serves to partition the variance attributable to repeated measures, nested designs, or clustering, allowing more accurate estimation of fixed effects and accounting for within-group correlation [1,17,18]. For instance, in avian behavioral studies, call frequency data may be clustered by nest or observation session, necessitating the inclusion of random intercepts or slopes at these levels. However, fitting Poisson and NB-GLMMs poses significant computational challenges. Although parameter estimation in GLMs is typically performed using iterative likelihood-based algorithms, GLMMs require additional numerical integration over the random effects because their marginal likelihoods do not have closed-form expressions. Among various estimation approaches, such as Laplace approximation or penalized quasi-likelihood (PQL), AGHQ has emerged as a leading technique due to its superior accuracy in small- to moderate-sized datasets and complex random structures [7–9]. In the present study, AGHQ is employed to estimate the Poisson GLMM, while the NB-GLMM is estimated using the Laplace approximation as implemented in glmmTMB.

AGHQ improves upon standard Gaussian-Hermite Quadrature (GHQ) by adaptively centering and scaling the quadrature node points around the mode of the integrand, thereby yielding more accurate approximations of marginal likelihoods and posterior moments [19]. This is particularly advantageous in ecological applications where sample sizes are limited and variance components are difficult to estimate precisely. Simulation studies have shown that AGHQ outperforms traditional methods in terms of bias reduction and standard error accuracy, especially when the data involve multiple levels of nesting or pronounced overdispersion [10,11].

For GLMMs, parameter estimation is based on the marginal likelihood obtained by integrating out the random effects,  $L(\beta, \theta) = \prod_{i=1}^m \int f(y_i|b_i, \beta)f(b_i|\theta)db_i$ , where  $f(y_i|b_i, \beta)$  denotes the conditional distribution of the response given the random effects and  $f(b_i|\theta)$  is the random-effects density. Since this marginal likelihood has no closed-form solution for Poisson and NB-GLMMs, AGHQ approximates the integral numerically as  $\int g(b)db \approx \sum_{k=1}^{nAGQ} w_k g(b_k)$ , where  $b_k$  are the quadrature nodes, and  $w_k$  are the corresponding weights. In the present study, AGHQ was implemented through the glmer() function to estimate the Poisson GLMM using  $nAGQ = 10, 15, 20$ , and  $25$  adaptive quadrature nodes, allowing assessment of the influence of numerical integration accuracy on parameter estimation and model fit.

In AGHQ approach, quadrature node placement is dynamically adjusted based on the current best estimates of the fixed effects, random effects, and their associated variance-covariance structure [10,12]. This data-driven positioning of the nodes concentrates computational effort in regions of the parameter space that contribute most to the likelihood, in contrast to classical GHQ, which employs fixed nodes centered around standard normal kernels. As a result, AGHQ can achieve high levels of approximation accuracy using fewer nodes, enhancing both efficiency and numerical precision.

A critical consideration in AGHQ is the selection of the number of quadrature nodes, as this directly impacts the accuracy of the integral approximation. While increasing the number of nodes typically improves the quality of the approximation—especially in models with non-normal, skewed, or heavy-tailed random effects distributions—it also imposes substantial computational overhead [20]. Beyond a certain threshold, the marginal gains in precision diminish, making further increases in node count inefficient in terms of resource consumption [21]. Therefore, an optimal balance must be struck between accuracy and computation time, particularly in large-scale or high-dimensional models.

Further constraints arise from the structural assumptions required by quadrature-based estimation in `glmer()`. Specifically, the function currently supports only a single scalar random effect when quadrature is used, and assumes a constant-variance covariance structure [12,13]. This restricts its applicability to more sophisticated random-effects configurations such as crossed or non-nested structures, or designs lacking clear subject identifiers. In such situations, Laplace approximation offers broader modeling flexibility and remains the method of choice. Nonetheless, when model complexity is moderate and assumptions are met, AGHQ consistently yields more precise parameter estimates than Laplace approximation [12].

In sum, the theoretical justification for NB-GLMMs lies in their ability to address overdispersion, account for hierarchical data structures, and provide robust inference in ecological studies. Nevertheless, whether the additional flexibility of the NB distribution translates into superior model performance should ultimately be evaluated empirically using appropriate model selection criteria.

### 3. Modeling Owl Nestling Behavior Strategy: Data and Variables

This study investigates the factors affecting the average number of calls produced by barn owl (*Tyto alba*) nestlings. Nestling vocal behavior has received considerable research attention, particularly in relation to sibling negotiation and begging calls associated with food. The dataset analyzed here originates from the work of [12,15], which explored how barn owl chicks adjust their begging behavior and vocal responses under different feeding conditions. Gaining a better understanding of these influences can shed light on sibling communication strategies and parental food allocation patterns.

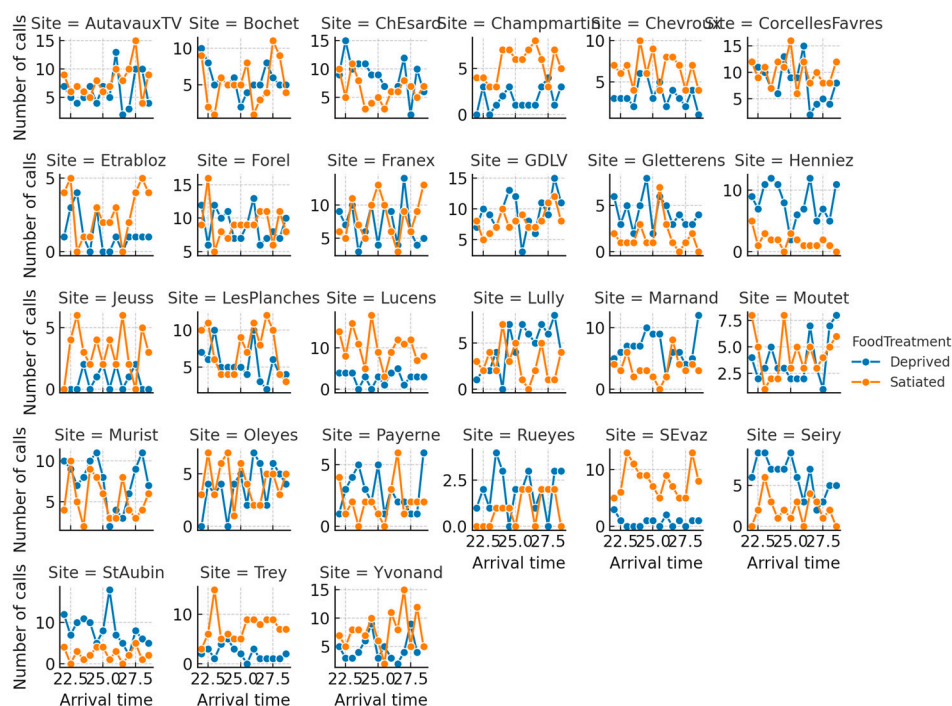
The dataset comprises 599 observations collected from 27 barn owl nests in western Switzerland during the summer of 1997 [12,15]. The number of observations per nest varies between 4 and 52. Each nest was fitted with both audio and video recording equipment to track the timing of parental arrivals and document nestling vocal activity. Adult owls were individually identified by leg bands (females on the left leg, males on the right) to allow monitoring of feeding rates and parent-specific interactions.

In the mornings (around 09:00), nestlings were subjected to one of two feeding treatments: a food-satiated group (given extra prey items by the researchers) and a food-deprived group (with remaining prey removed from the nest). Observations took place overnight (21:30–05:30), during which parental feeding events were recorded, including arrival times, time spent in the nest, and call frequency of the chicks. Previous findings [15] indicate that sibling negotiation is a key component of competition for food among nestlings. Pre-arrival calls are believed to signal hunger levels and may influence how food is distributed within the brood.

Earlier studies have revealed several notable patterns: chicks may adjust their calling intensity depending on whether the arriving parent is the mother or the father; well-fed nestlings tend to reduce calling to avoid unnecessary competition and conserve energy; and food-deprived nestlings show substantially higher call rates, supporting the view that vocal activity is closely linked to hunger state.

In this study, sibling negotiation is quantified as the number of calls produced by a chick in the 30 s prior to a parent's arrival, and this serves as the dependent variable. Below are some graphical summaries of the barn owl nestling dataset.

Figure 1 presents the temporal dynamics of calls during sibling negotiation. The figure displays how the number of calls varies over time across multiple nest sites, grouped by food treatment ("Deprived" vs. "Satiated"). The  $x$ -axis shows arrival time, and the  $y$ -axis indicates the call count for each site. Overall, the results suggest that food treatment influences calling behavior: in many nests, deprived chicks produce more calls than satiated chicks, particularly at earlier arrival times. Nonetheless, this trend is not uniform across all sites, reflecting considerable variation in sibling negotiation patterns among nests.

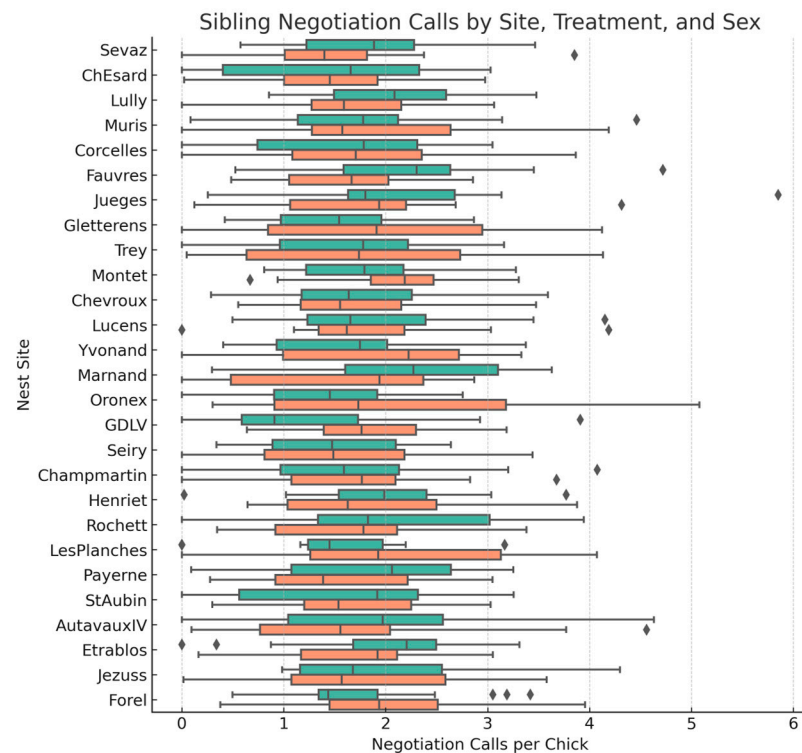


**Figure 1.** Temporal dynamics of sibling negotiation calls across barn owl nests. The  $x$ -axis represents parental arrival time, while the  $y$ -axis shows the number of calls produced by nestlings. Panels correspond to individual nest sites, and colors distinguish the two feeding treatments (deprived and satiated).

Boxplot of sibling negotiation calls across nest sites by sex is given by Figure 2. This boxplot displays the distribution of sibling negotiation calls per chick across different nest sites, separated by sex (female and male). The  $x$ -axis shows the number of calls per chick, while the  $y$ -axis lists the nest sites. The colors differentiate between sexes. In general, there is noticeable variation in the frequency of calls among sites, and certain sites show higher median values than others. Although patterns differ across sites, in several cases, males tend to produce slightly more calls than females. The spread of the data also suggests variability in calling behavior, with some nests exhibiting a wider range of negotiation calls than others.

Because nestlings within the same nest tend to exhibit correlated calling behaviors due to shared genetic, environmental, and social factors, nest identity was modeled as a random intercept to account for the hierarchical data structure. The response variable, representing the discrete number of calls per observation interval, was initially assumed to follow a Poisson distribution, which is the conventional choice for count data [5]. To evaluate the adequacy of the Poisson assumption, overdispersion was assessed using the Pearson dispersion statistic. The estimated dispersion ratio was 4.45, indicating that the

observed variance exceeded that expected under the Poisson distribution. Consequently, a NB-GLMM was also fitted to account for the observed overdispersion. A random intercept for nest identity was included to account for the correlation among observations within the same nest. The final comparison between the Poisson and Negative Binomial GLMMs was based on Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and log-likelihood values to determine the model providing the best overall fit to the data. Although evidence of overdispersion was detected, the Poisson GLMM consistently produced lower AIC and BIC values than the NB-GLMM, indicating that the additional flexibility of the NB distribution did not improve model fit for the present dataset.



**Figure 2.** Boxplots of sibling negotiation call counts across barn owl nest sites by sex. The x-axis represents the number of calls recorded during the 30 s preceding parental arrival, whereas the y-axis identifies the nest sites. Colors distinguish female and male nestlings, illustrating variation in call distributions among nests and between sexes.

The owl nestlings dataset is analyzed using the following statistical model

$$\log(\mu_{ij}) = \beta_0 + \beta_1 \log(\text{BroodSize}_{ij}) + \beta_2 \text{FoodTreatment}_{ij} + \beta_3 \text{ArrivalTime}_{ij} + \text{Nest}_i.$$

where  $i = 1, \dots, m$  indexes the nests and  $j = 1, \dots, n_j$  indexes the observations within nest  $i$ . Here,  $\mu_{ij}$  denotes the conditional mean call count for observation  $j$  in nest  $i$ , and  $\text{Nest}_i$  represents the random intercept associated with nest  $i$ .

In this model, the response variable ( $\mu_{ij}$ ) corresponds to the mean number of calls, measured as the vocalizations of chicks within 30 s prior to the parent's arrival. The explanatory variables (fixed effects) consist of the log-transformed brood size ( $\log(\text{BroodSize}_{ij})$ ), the feeding condition ( $\text{FoodTreatment}_{ij}$ ), and the parental arrival time ( $\text{ArrivalTime}_{ij}$ ). To account for differences between nests, a random intercept for nest ( $\text{Nest}_i$ ) is included [22]. In contrast to [22], whose primary aim was to compare estimation techniques (Laplace vs. AGHQ) within the Poisson GLMM framework, our focus lies in evaluating the suitability of alternative distributional assumptions (e.g., Poisson or NB) for modeling the call counts.

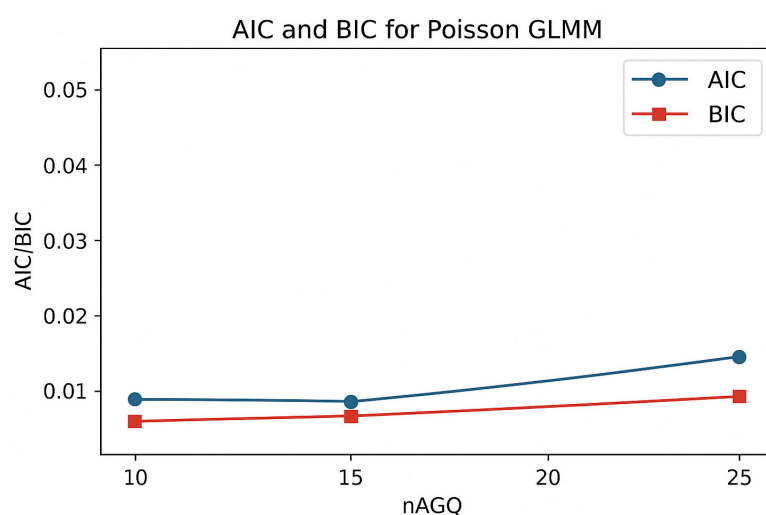
## 4. Results

In this section, estimation for the Poisson GLMM is performed via `glmer()` with varying numbers of quadrature nodes ( $nAGQ = 10, 15, 20$ , and  $25$ ), while the NB-GLMM is estimated via `glmmTMB()` using the Laplace approximation. This setup allows for a systematic evaluation of model performance under different levels of numerical precision. Model comparison between the Poisson and NB-GLMMs is conducted using information criteria AIC and BIC, enabling assessment of relative model fit and the impact of overdispersion on inference.

Table 1 presents the Poisson GLMM results estimated via AGHQ with different numbers of quadrature points ( $nAGQ = 10, 15, 20, 25$ ). The AIC, BIC, and log-likelihood values remain almost identical across all settings, with differences only in the order of  $10^{-5}$ . This stability indicates that increasing the number of quadrature points beyond 10 does not meaningfully improve model fit. Figure 3 further illustrates these findings by plotting the relative differences ( $\Delta AIC$  and  $\Delta BIC$ ) with respect to the minimum observed value for each criterion. The curves show that both AIC and BIC vary negligibly as  $nAGQ$  increases, underscoring the robustness of the Poisson GLMM estimation with AGHQ. In practical terms, this suggests that using  $nAGQ = 10$  is sufficient to achieve reliable results while maintaining computational efficiency.

**Table 1.** Poisson GLMM results estimated via AGHQ ( $nAGQ = 10, 15, 20, 25$ ) [22].

| Model                          | AIC/BIC                   | Log-Likelihood |
|--------------------------------|---------------------------|----------------|
| owl_glmer_AGHQ ( $nAGQ = 10$ ) | 2231.9485911/3634.0370409 | −796.9742955   |
| owl_glmer_AGHQ ( $nAGQ = 15$ ) | 2231.9486062/3634.0370560 | −796.9743031   |
| owl_glmer_AGHQ ( $nAGQ = 20$ ) | 2231.9486075/3634.0370573 | −796.9743037   |
| owl_glmer_AGHQ ( $nAGQ = 25$ ) | 2231.9486075/3634.0370573 | −796.9743037   |



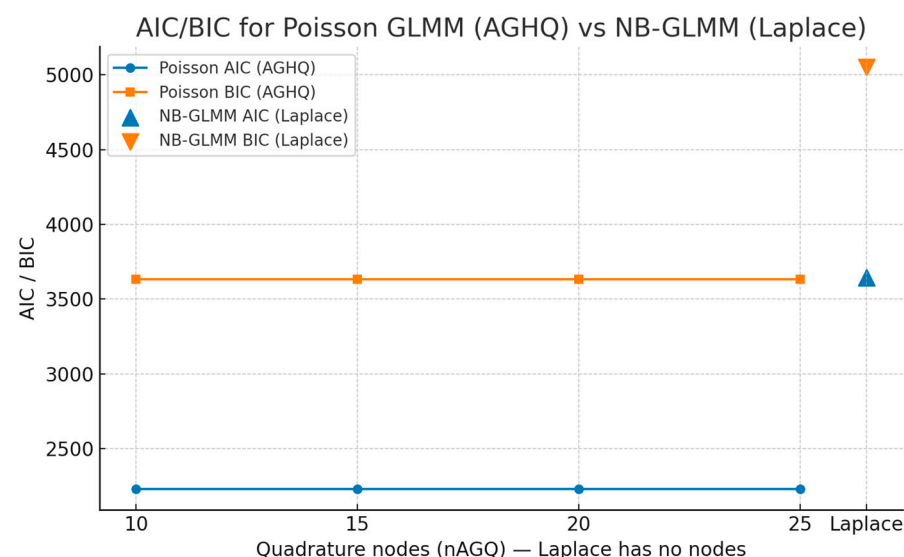
**Figure 3.** Differences in AIC and BIC across  $nAGQ$  for Poisson GLMM.

Table 2 indicates the NB-GLMM results estimated via Laplace approximation.

**Table 2.** NB-GLMM results estimated via Laplace approximation.

| Model               | AIC/BIC                   | Log-Likelihood |
|---------------------|---------------------------|----------------|
| owl_glmmTMB_Laplace | 3643.8820000/5050.3660000 | −1501.9410000  |

In Figure 4, the comparison of model fit based on AIC and BIC values provides important insights into the relative performance of the Poisson GLMM estimated via AGHQ and the NB-GLMM estimated via the Laplace approximation. The results show that, across increasing numbers of quadrature nodes ( $n_{AGQ} = 10, 15, 20, 25$ ), both the AIC and BIC values for the Poisson GLMM remain virtually unchanged, indicating stable estimates and convergence of the approximation method. This stability implies that further increases in the quadrature points do not yield additional improvements in model fit, confirming the robustness of the Poisson GLMM under AGHQ estimation. In contrast, the NB-GLMM estimated via the Laplace approximation yields substantially larger AIC and BIC values, suggesting a poorer fit relative to the Poisson specification. Since both AIC and BIC penalize model complexity while rewarding goodness-of-fit, the consistently lower values obtained for the Poisson GLMM indicate that this model provides a more parsimonious and efficient representation of the data. Although the overdispersion diagnostic indicated extra-Poisson variation (dispersion ratio = 4.45), the Poisson GLMM consistently achieved lower AIC and BIC values than the NB-GLMM. This finding suggests that, for the present dataset, the additional flexibility provided by the NB distribution did not improve overall model fit. Therefore, the Poisson GLMM estimated via AGHQ was selected as the preferred model according to the adopted model selection criteria, offering both computational stability and superior goodness-of-fit.



**Figure 4.** Comparison of AIC and BIC values for Poisson GLMM estimated via AGHQ ( $n_{AGQ} = 10, 15, 20, 25$ ) and NB-GLMM estimated via the Laplace approximation.

The comparison of log-likelihood values across Poisson GLMM (AGHQ) and NB-GLMM (Laplace) provides further insight into model fit. As reported in Table 1, the Poisson GLMM estimated via AGHQ with varying numbers of nodes ( $n_{AGQ} = 10, 15, 20, 25$ ) produced almost identical log-likelihood values around  $-796.97$ , indicating numerical stability and insensitivity to the choice of quadrature nodes. In contrast, the NB-GLMM estimated with the Laplace approximation (Table 2) yielded a much lower log-likelihood of approximately  $-1501.94$ , suggesting a substantially poorer fit relative to the Poisson specification.

This discrepancy highlights two key points. First, despite the theoretical advantage of NB-GLMM in handling overdispersion, the observed differences may reflect both the choice of distribution and the estimation approach used for model fitting. Second, the AGHQ approach provides more precise likelihood estimation, as evidenced by the consistency across different node values, whereas the Laplace approximation offers greater

computational efficiency. Consequently, the Poisson GLMM estimated via AGHQ emerged as the preferred model according to the adopted likelihood-based model selection criteria.

Accordingly, the findings should be interpreted within the estimation frameworks adopted in this study rather than as a general conclusion regarding the superiority of one distribution over another. Although the comparison was conducted using estimation methods that are commonly employed for the respective models, future studies may further extend this work by evaluating both distributions under identical estimation strategies, for example by fitting both Poisson and NB-GLMMs using AGHQ where computationally feasible. Nevertheless, the present comparison provides practical guidance for selecting appropriate GLMM specifications for hierarchical ecological count data under commonly adopted estimation approaches.

The present study adopted a random-intercept GLMM framework to facilitate a consistent comparison between the Poisson and NB specifications under commonly adopted estimation approaches. Although this modeling framework accounts for the hierarchical dependence among observations within nests, it does not explicitly model more complex sources of heterogeneity, such as temporal dependence, random slopes, sibling interactions, parental identity, or nest-level environmental characteristics. These factors may contribute additional variability and represent important directions for future research using more comprehensive hierarchical modeling frameworks. Accordingly, the conclusions of the present study should be interpreted within the scope of the adopted random-intercept GLMM specification.

## 5. Conclusions

In this study, we revisited the barn owl (*Tyto alba*) nestling call count dataset to evaluate the suitability of Poisson and NB-GLMMs in capturing the dynamics of sibling negotiation and vocal behavior. By explicitly accounting for the hierarchical structure of the data through a random intercept for nest identity, we were able to rigorously assess the performance of each model under realistic ecological conditions.

Our findings indicate that the Poisson GLMM estimated via AGHQ provides a stable and robust fit to the data. Across varying numbers of quadrature nodes ( $n_{AGQ} = 10, 15, 20$ , and 25), model fit metrics, including AIC, BIC, and log-likelihood, remained virtually unchanged, demonstrating numerical stability and insensitivity to the number of quadrature nodes. In contrast, the NB-GLMM estimated via the Laplace approximation yielded higher AIC and BIC values and lower log-likelihoods, indicating a poorer overall fit despite its theoretical advantage in modeling overdispersed count data. Although the overdispersion diagnostic (Pearson dispersion ratio = 4.45) indicated extra-Poisson variation, the Poisson GLMM consistently outperformed the NB-GLMM according to the adopted model selection criteria (AIC, BIC, and log-likelihood). These findings suggest that, for the present dataset, the additional flexibility of the NB distribution did not improve overall model fit, and the simpler Poisson GLMM provided the most parsimonious and best-fitting representation of the data.

The study also highlights the practical importance of estimation methods in hierarchical count models. AGHQ provides a more accurate approximation to the marginal likelihood than the Laplace method, particularly in datasets with moderate sample sizes and hierarchical structures. While NB-GLMMs remain a valuable tool for overdispersed or zero-inflated data, our findings demonstrate that the presence of overdispersion alone does not necessarily imply that a NB model will provide the best overall fit. Instead, careful consideration of model assumptions, distributional characteristics, estimation methods, and likelihood-based model selection criteria is essential when selecting an appropriate modeling framework.

Beyond the empirical comparison presented here, this study demonstrates that evidence of overdispersion should not be regarded as the sole criterion for selecting a NB-GLMM, emphasizing the importance of jointly evaluating distributional assumptions, estimation methods, and likelihood-based model selection criteria.

From an ecological perspective, these findings suggest that model selection for hierarchical count data should not rely solely on the presence of overdispersion, but should also consider model assumptions, estimation methods, and likelihood-based model selection criteria. These findings also have practical implications for ecological studies based on hierarchical count data, indicating that the selection of an appropriate GLMM should be guided by empirical model performance in addition to theoretical distributional assumptions. In ecological and behavioral research, these findings further emphasize that simpler models—when supported by appropriate data diagnostics and model selection criteria—can offer both computational efficiency and reliable inference. Future research may build on the present study by considering more comprehensive hierarchical model structures and expanding comparisons to a wider range of alternative modeling approaches.

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