Genetic Parameters for Feather Pecking and Aggressive Behavior in Laying Hens Using Poisson and Linear Models

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ABSTRACT: An F2-design was established from two divergent selected founder laying hen lines, which included 910 F2-hens. Each pen was observed in 21 sessions of 20 min each, distributed over three consecutive days. An animal model was applied that treated the bouts observed within 20 minutes (short period) or the summed bouts within one day (medium period) as repeated observations. A dispersed Poisson distribution was assumed. Residual variance was approximated on the link scale by the delta method. The estimated variance components were on a similar level for the two observation periods, except the approximated residual variance. This was substantially smaller for the medium period, leading to lower heritabilities on the link scale for the short period compared to the medium period (0.11 vs. 0.19 for feather pecking and 0.09 vs. 0.24 for aggressive pecking). Variance components were also estimated using a linear model.
Keywords: Feather pecking; Generalized linear model; Heritability

Introduction

Feather pecking in laying hens is characterized by non-aggressive pecks directed towards the plumage of other hens. The underlying mechanisms are not well understood, but physiological, nutritional as well as genetic factors are known to influence this trait (Wysocki et al. (2010)). Quantitative genetic analyses have revealed low to moderate heritabilities (Kjaer et al. (2001); Rodenburg et al. (2003)). Aggressive pecking is clearly distinguishable from feather pecking. Aggressive pecks are delivered in an upright body posture and are mainly directed towards the head of the recipient birds (Kjaer et al. (2001)).

Feather pecking and aggressive pecking are recorded by observation of the hens in defined time periods. The observations are count values with large proportions of zero counts. The latter one makes it difficult and in most cases impossible to obtain a normal distribution by a data transformation. The use of generalized linear mixed models (GLMM) to analyze the data is an appropriate way to account for the non-normal distribution of the data. In a recent study we used dispersed Poisson models to estimate variance components, heritabilities and approximate genetic correlations for behavior traits in a large F2 cross of laying hens (Bennewitz et al. (2014)). The aim of the present study was to extent these analyses towards different observation periods. In addition, the data were analyzed with a standard linear model.

Materials and Methods

Data collection and editing. Starting from a founder generation, two lines were divergently selected for low respectively high feather pecking. From the 10th selection generation an F1-cross was generated using an equal number of birds from each line. These were mated reciprocally with males or females from the other line in order to generate 10 F1-families. From these families an F2-cross was established, which consisted of 10 F2 paternal half-sib families with an average number of 91 female offspring, and in 910 hens in total. Behavioral data collection started at 27 weeks of age. The group size varied between 36 and 42 birds. Seven experienced observers recorded feather pecking and aggressive pecking within each pen during sessions of 20 min each. Each pen was observed for 140 minutes per day and over three consecutive days making a total of 21 sessions of 20 min. All incidences (bouts) of feather pecking and aggressive pecking were recorded. For each bout, the identity of the actor and receiver was recorded. This resulted in four behavior traits: bouts of feather pecking delivered (**FPD**), bouts of feather pecking received (**FPR**), bouts of aggressive pecking delivered (**APD**) and bouts of aggressive pecking received (**APR**). FPR showed a additive genetic variance of almost zero (Bennewitz et al. (2014)) and therefore was not considered in this study.

Data analysis using GLMM. The number of recorded pecks and received pecks, respectively, in each 20 min observation period (short period) and in each observation day (medium period), were modeled as repeated observations in the statistical analysis with the GLMMs. There were 21 repeated observations for the short period and in three repeated observations for the medium period per hen. Because the observations were count values they were initially assumed to be Poisson distributed and were analyzed with the following GLMM. For the short period the linear predictor was:

$$\eta = Xb + Z_{pen}pen + Z_{pe}pe + Z_{de}de + Z_a a$$

where *b* is a vector of fixed effects (short period: observer, test-day and observer-by-test-day interaction; medium period: test-day), *pen* is a vector with random pen effects, *pe* is a vector with random permanent environment effects of the hens, *de* is a vector of random test-day-by-hen effects (only for the short period), *a* is a vector with the random additive-genetic effects, and X, Z_{pen}, Z_{pe}, Z_{de}, and Z_a are known design matrices. The covariance structure of the

random effects were $\text{var}(pen) = I * \sigma_{pen}^2$ $\text{var}(pe) = I * \sigma_{pe}^2$, $\text{var}(de) = I * \sigma_{de}^2$, and $\text{var}(a) = A * \sigma_a^2$, where σ_{pen}^2, σ_{pe}^2, σ_{de}^2, and σ_a^2 are pen variance, permanent environmental variance, test-day-by-hen variance, and additive genetic variance respectively, and A (I) is the numerator relationship (identity) matrix. For the medium period the same linear predictor was used, but without the de effect. The expectations of the observations were $\lambda = E(y \mid pen, a, pe, de) = g^{-1}(\eta)$ (short period) and $\lambda = E(y \mid pen, a, pe) = g^{-1}(\eta)$ (medium period), where g is the link function, in this case a log link, i.e. $g = \log_e(\eta)$. As we detected over dispersion relative to the Poisson model, a dispersion parameter (ϕ) was added to the models on the observed scale by assuming the variance function $\text{var}(y \mid pen, a, pe, de) = \lambda\phi$ (short period) and $\text{var}(y \mid pen, a, pe) = \lambda\phi$ (medium period). Unlike in linear mixed models, calculating the repeatability and heritability from the variance components is not straightforward for GLMMs. This is because it is not obvious how the residual variance can be obtained under a Poisson model. Based on the Delta method we approximated the residual variance as $\phi\lambda^{-1}$, which is an extension of the approach of Foulley et al. (1987) towards accounting for $\phi \neq 1$ (see Bennewitz et al. (2014)). Following this, the heritability on the η scale for the short period was computed according to:

$$h^2 = \frac{\sigma_a^2}{\sigma_{pen}^2 + \sigma_a^2 + \sigma_{pe}^2 + \sigma_{de}^2 + \phi\lambda^{-1}} .$$

The Poisson parameter λ was estimated for each subject and then averaged over all subjects. The repeatability was $t = (\sigma_a^2 + \sigma_{pe}^2)/(\sigma_a^2 + \sigma_{pen}^2 + \sigma_{pe}^2 + \sigma_{de}^2 + \phi\lambda^{-1})$. For the medium period the same computations were performed, but without σ_{de}^2.

Data analysis using linear mixed models. For this analysis the observations were accumulated over the entire observation period of 420 min (long period), result-ing in one observation per hen. The following linear model was used:

$$y = Xb + Z_{pen}pen + Z_a a + e ,$$

where the fixed effect included the hatch, e denotes for the residual term and the remaining terms are as defined above. This analysis was conducted, because it is a standard analysis of feather pecking data. It is noted, that an analysis of this data set by a Poisson model led to convergence problems and hence was not possible. All models were fitted for each trait separately using ASReml 3.0 (Gilmour et al. (2009)).

Results and Discussion

The histograms of the traits revealed that they are not normally distributed and that there are large proportions of zero counts, especially fro the short period (not shown). The results of the GLMM analysis are shown in Table 1. The variance components were remarkably on a similar level for both observation periods. However, the residual variance was substantially smaller for the medium period, leading to a higher heritability and repeatability for this period. For the short period the heritability is in between 0.04 (APR) and 0.11 (FPD). For the medium period it varied between 0.14 (APR) and 0.24 (APD). The higher residual variance for the short period is due to a small average Poisson parameter λ, which over-compensated the effect of the smaller dispersion parameter ϕ for this period (Table 1). This possibly yielded downward biased heritability estimates for the short period. Maybe a distribution which is able to model the excess of zero counts explicitly would be more appropriate for the short period, e.g. a zero-inflated Poisson distribution.

A remarkable result is the high permanent environment effect for the traits, especially for FPD and APD, which was not reported so far. This indicates that if hens delivered feather pecks or aggressive pecks once, they might continue in doing this. But also for the trait APR there is a substantial permanent environment effect. This implies that once hens were identified as 'victims' they

Table 1. Estimated additive genetic variance ($\hat{\sigma}_a^2$), permanent environment variance ($\hat{\sigma}_{pe}^2$), test-day-by-hen variance ($\hat{\sigma}_{de}^2$), pen variance ($\hat{\sigma}_{pen}^2$), dispersion parameter ($\hat{\phi}$), residual variance ($\chi^{-1}\hat{\phi}$), heritability ($\hat{h}^2$), and repeatability ($\hat{t}$) for the behaviour traits (standard errors are shown in parenthesis), results from the GLMMs

Feather pecks delivered, FPD		Aggressive pecks delivered, APD		Aggressive pecks received, APR	
Short period	Medium period	Short period	Medium period	Short period	Medium period
0.46 (0.18)	0.49 (0.19)	0.42 (0.13)	0.41 (0.13)	0.17 (0.06)	0.18 (0.06)
1.40 (0.15)	1.33 (0.14)	0.53 (0.09)	0.52 (0.09)	0.30 (0.05)	0.34 (0.05)
0.62 (0.03)	-	0.35 (0.03)	-	0.25 (0.03)	-
<0.001	<0.001	0.03 (0.02)	0.02 (0.02)	0.05 (0.02)	0.03 (0.02)
1.13 (0.01)	3.27 (0.08)	0.79 (0.01)	1.37 (0.04)	0.85 (0.01)	1.29 (0.04)
1.85	0.80	3.04	0.76	3.40	0.75
0.11	0.19	0.09	0.24	0.04	0.14
0.43	0.56	0.22	0.54	0.12	0.40

stayed within this category. On the other hand, there are hens that successfully avoid receiving pecks.

Table 2. Estimated additive genetic variance ($\hat{\sigma}_a^2$), residual variance ($\hat{\sigma}_e^2$), pen variance ($\hat{\sigma}_{pen}^2$), and heritability ($\hat{h}^2$) for the behavior traits (standard errors are shown in parenthesis), results from the linear model

Item	FPD, long period	APD, long period	APR, long period
$\hat{\sigma}_a^2$	93.93 (40.84)	15.26 (4.81)	7.30 (2.43)
$\hat{\sigma}_e^2$	573.89 (38.12)	40.81 (3.52)	19.39 (1.74)
$\hat{\sigma}_{pen}^2$	<0.001	0.50 (0.53)	1.06 (0.78)
$\hat{h}^2$	0.14 (0.06)	0.27 (0.08)	0.27 (0.08)

Table 3. Pearson correlation coefficients between animal effects obtained from different models[§]

Trait	short - medium period	short - long period	medium - long period
FPD	0.99	0.92	0.93
APR	0.99	0.96	0.96
APD	0.99	0.93	0.94

[§] Animal effects of the short period and medium period were obtained from the GLMMs and of the long period from the linear model

The results of the linear model and the long period are shown in Table 2. The heritability on the observed scale is 0.16, 0.26 and 0.27 for FPD, APD and APR, respectively. These figures are higher compared to the heritabilities obtained from the GLMM for the short period, but note that a formal comparison is not valid. The disadvantage of accumulating the bouts across the entire observation period, as done for the long period, is that it is not possible to separate random additive animal effects from permanent environment effects. The Pearson correlation coefficients between the random animal effects obtained from the three models are shown in Table 3. These are high, especially for the effects obtained from the two GLMMs. The correlations suggest that re-ranking of individuals might be an issue only if predictions of the linear model and the GLMMs are compared.

Behavior traits depend on the interactions among individuals. Models were developed that include interaction or associated effects (see Bijma (2013) and references therein). As suggested by Bijma (2013), we chose the simplest form to capture shared environment effects and associated effects by fitting a random pen effect to the GLMMs. The pen variances were small (Table 1 and 2), but interpreting the magnitude of associated effects is not trivial (Bijma (2013)).

Conclusions

The estimated variance components showed a relatively small standard error. This is due to the thorough observations of the traits using a standardized protocol. In addition it implies that the data set was of sufficient size to obtain accurate estimates. The permanent environment effects were substantial for all traits. Accounting for over-dispersion in the Poisson models was important. The heritability of the traits was low to medium, depending on the period considered and on the models used. Modelling the data as repeated observations (short and medium period) and analysing them with a dispersed Poisson model is a suitable option to separate the important permanent environment effects from the additive animal effects and to account for the non-normal distribution of the data.

Acknowledgements

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