

GENETICS

Variance Components and Selection Response for Feather-Pecking Behavior in Laying Hens

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ABSTRACT Variance components and selection response for feather pecking behavior were studied by analyzing the data from a divergent selection experiment. An investigation indicated that a Box-Cox transformation with power $\lambda = -0.2$ made the data approximately normally distributed and gave the best fit for the model. Variance components and selection response were estimated using Bayesian analysis with Gibbs sampling technique. The total variation was rather large for the investigated traits in both the low feather-pecking line (LP) and the high feather-pecking line (HP). Based on the mean of marginal posterior distribution, in the Box-Cox transformed scale, heritability for number of feather pecking

bouts (FP bouts) was 0.174 in line LP and 0.139 in line HP. For number of feather-pecking pecks (FP pecks), heritability was 0.139 in line LP and 0.105 in line HP. No full-sib group effect and observation pen effect were found in the 2 traits. After 4 generations of selection, the total response for number of FP bouts in the transformed scale was 58 and 74% of the mean of the first generation in line LP and line HP, respectively. The total response for number of FP pecks was 47 and 46% of the mean of the first generation in line LP and line HP, respectively. The variance components and the realized selection response together suggest that genetic selection can be effective in minimizing FP behavior. This would be expected to reduce one of the major welfare problems in laying hens.

(*Key words:* feather pecking, selection, heritability, Box-Cox transformation, poultry welfare)

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INTRODUCTION

Feather pecking (FP) is characterized as pecking at and pulling out of feather of conspecifics. It is thought to be a form of redirected behavior, originating from ground pecking (Blokhuys, 1986), dust-bathing (Vestergaard and Lisborg, 1993), or socially related pecking (Riedstra and Groothuis, 2002). The physiological mechanisms are not well known, but there is evidence that birds with a strong tendency to perform FP have some kind of malfunction in the dopamine system. Treatment with haloperidol, a dopamine D2 receptor antagonist, was found to reduce FP (Kjaer et al., 2004). Feather pecking can have a range of harmful consequences. Feather removal is painful to the birds (Gentle and Hunter, 1990) and FP appears to be associated with fearfulness (Hughes and Duncan, 1972). Panic and fearful reactions to FP can cause trampling (Mills and Faure, 1990). Feather pecking sometimes leads to cannibalism and this can result in high mortality (Appleby et al., 1992; Savory, 1995; Kjaer and Sørensen, 2002). Feather pecking can cause extensive feather dam-

age and consequently a loss of heat, thus leading to higher feeding costs (Tauson and Svensson, 1980; Blokhuys and Wiepkema, 1998).

To reduce the harmful effects of FP, beak trimming of birds is widely used in poultry production. However beak trimming itself causes pain and suffering (Gentle, 1986; Duncan et al., 1989; Gentle et al., 1990; Hester and Sheamoore, 2003). An alternative approach to reduce FP behavior is genetic selection. Many investigations have found a variation in FP behavior between strains and between family groups (Richter, 1954; Hughes and Duncan, 1972; Tind and Ambrosen, 1988; Craig and Lee, 1990; Kjaer, 2000). Low to moderate heritabilities (h^2) for FP have been reported (Cuthbertson, 1980; Bessei, 1984; Kjaer and Sørensen, 1997; Rodenburg et al., 2003). These results indicate that there is a genetic basis for FP behavior.

Genetic change of the tendency to perform injurious pecking has been demonstrated. Using group selection, the incidence of beak-inflicted injuries, causing feather loss and cannibalism, was reduced after one generation of selection (Craig and Muir, 1993), and greatly reduced after 6 generations of selection (Muir, 1996). Using diver-

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Abbreviation Key: FP = feather pecking; h^2 = heritability; HP = high feather pecking line; LP = low feather pecking line; REML = restricted maximum likelihood

gent selection for number of FP bouts, Kjaer et al. (2001) obtained a high and a low feather-pecking line.

To properly plan and conduct a selection program, unbiased estimates of genetic parameters are required. In general, FP data are quite far from a normal distribution. Current methods to estimate genetic parameters, however, usually assume that data, either in original scale or on an underlying scale, are normally distributed. Therefore, a proper transformation making the data normally distributed should be carried out to get an unbiased estimate of the genetic parameters. Several transformations can be used for this purpose. One of the most common methods is the Box-Cox power transformation (Box and Cox, 1964).

Response to selection can be evaluated by least square means if proper control lines are available. Otherwise, response to selection can be estimated as contrasts between generation means of the additive genetic values obtained with the mixed model equations based on animal models. Methods based on animal models include 2 approaches. The first is a 2-stage procedure (Sorensen and Kennedy, 1986; Harville, 1990), whereby variances are estimated first and then used in lieu of the true parameters to solve the mixed-model equations. In this approach, inferences about selection response ignore the uncertainty associated with the estimated variances. The second approach is to make use of Bayesian methods in which all parameters in the model are estimated simultaneously, thereby accounting for the uncertainty of all other parameters of the model (Sorensen et al., 1994).

The objective of the present study was to investigate genetic variation in FP behavior and genetic change of this trait by selection, by analyzing the data from a divergent selection experiment. In the analysis, the data were transformed using Box-Cox power transformation. Variance components and selection response were estimated using Bayesian methods with Gibbs sampling and based on an animal model.

MATERIALS AND METHODS

The Populations and Selection Experiment

The data were collected from 2 experimental lines: line LP was selected for low FP, and line HP for high FP. The lines were established in 1995 and derived from a White Leghorn layer line formed in 1970. In the common base population, 123 hens were assessed for FP behavior at 67 wk of age. Then, the 30 females and 10 males with the highest breeding value of FP activity were selected as the founder animals of line HP, and the 30 females and 10 males with lowest breeding value were selected as the founder animals of line LP.

In the subsequent generations, a consistent selection procedure was followed. In each generation, at about 30 wk of age, females were transferred from cages to floor pens. Pen size was 2 × 4 m, and each pen held 20 females. After a settling-in period of 7 to 12 d, FP behavior of the females was recorded by video camera for 3 h. During

the measuring period, incandescent light was supplied with light intensity of approximately 25 lx at ground level. Feather-pecking behavior of individual hens was recorded from the tapes by counting the number of feather pecks (FP pecks) and grouping these into FP bouts (FP bouts). An FP bout was defined as a series of continuous pecks directed to the same recipient hen. Selection was based on the number of FP bouts. In each generation, 10 males (from about 50) and 30 females (from about 200) were selected as breeding birds in each line, based on breeding value, which was estimated using an animal model.

The selected birds were placed in individual cages and artificial insemination was conducted twice a week during the period of collecting eggs for hatching. All the eggs were pedigreed. The newly hatched chicks were tagged with identification bands in the wing and randomly distributed into floor pens. Birds in the 2 lines were mixed in the floor pens. At 18 wk, the birds were transferred to battery cages with 4 pullets in a cage and each male in a single-bird cage. The pullets in 1 cage came from the same line, but the cages with line LP or line HP birds were balanced over rows and within rows. Feed and water were supplied ad libitum during the experiment. The diets for 0 to 5 wk, 6 to 15 wk, and after 16 wk had crude protein content of 20.5, 13.2, and 16.4%, and an energy content of 2,771, 2,842, and 2,651 kcal/kg, respectively.

The data set in the present study covered generations 1 to 5 but excluded the observations for generation 0 (the common base population), because FP behavior was measured at 67 wk in this generation. As shown by Kjaer and Sørensen (1997), genetic correlation in FP behavior at 38 and 69 wk is about 0.5. The genetic correlation indicates that FP behavior measured at 67 wk in generation 0 and at about 30 wk of age in the following generation should be taken as 2 different traits. Thus, observations of FP in the data set came from 1,050 females in line LP and 1,060 females in line HP. For a more detailed description of the experiment and the testing procedure of feather pecking, see Kjaer et al. (2001).

Statistical Analysis

The data were analyzed separately for each trait (number of FP bouts and number of FP pecks) and each line (LP and HP). The following model was used to describe the component effects of an individual observation:

$$y = Xb + Z_c c + Z_f f + Z_a a + e$$

where y is the vector of number of bouts or number of pecks in Box-Cox transformation scale (Box and Cox, 1964), b is the vector of year-hatch effects, c is the vector of random effects of observation pens, f is the vector of full-sib group effects, a is the vector of additive genetic values, e is the vector of random residuals, and X , Z_c , Z_f , Z_a are known design matrices associating b , c , f , and a to y . The random effects were assumed normally distributed:

TABLE 1. Number of hens observed (n), mean, and SD for number of feather pecks (FP peck) and number of feather pecking bouts (FP bout) in each generation for the line selected for low feather pecking (LP) and the line selected for high feather pecking (HP)

Generation	Line LP					Line HP				
	n	FP peck		FP bout		n	FP peck		FP bout	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
1	193	10.75	22.52	2.82	6.15	200	7.46	14.76	2.42	5.31
2	260	10.26	29.33	4.12	12.3	225	19.22	44.18	9.08	24.54
3	193	7.71	23.17	2.02	5.63	219	40.95	95.22	13.13	39.23
4	220	7.00	19.22	1.84	4.96	133	20.29	40.42	4.88	7.76
5	194	6.32	14.99	1.13	1.86	273	51.79	199.56	6.03	13.36
Average	1,060	8.41	21.85	2.39	6.18	1,050	27.94	78.83	7.11	18.04

$$\mathbf{c} \sim N(\mathbf{0}, \mathbf{I}\sigma_c^2), \mathbf{f} \sim N(\mathbf{0}, \mathbf{I}\sigma_f^2), \mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2), \text{ and } \mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2),$$

where σ_c^2 , σ_f^2 , σ_a^2 , and σ_e^2 are variance of observation pen effects, full-sib group effects, additive genetic values, and random residuals, respectively, \mathbf{I} is the identity matrix of appropriate order, and \mathbf{A} is the matrix of genetic relationships.

The Box-Cox transformation was done as

$$y_t = \frac{(y^\lambda - 1)}{\lambda}, \text{ for } \lambda \neq 0, y_t = \log(y), \text{ for } \lambda = 0, (y > 0)$$

where y is number of FP bouts or number of FP pecks in original scale plus 1 (to meet $y > 0$). A set of λ ranging from -1 to 1 with interval 0.1 was used to do the transformation. An approximate optimal value of λ was obtained by judging the normality and the maximum likelihood based on the transformations with different values of λ . The normality was evaluated by skewness and kurtosis for the transformed data after accounting for year-hatch effects. The maximum likelihood was obtained using REML (restricted maximum likelihood) procedure with the package DMU (Jensen and Madsen, 1993) based on the above model.

Variance components and breeding values were estimated using a Bayesian analysis with Gibbs sampling technique (Korsgaard et al., 2003) based on the transformation with the approximate optimal value of λ . In the Bayesian analysis, the prior distribution of fixed effects and variance components was assumed uniformly distributed. The Gibbs sampler was run using a single chain of length 250,000. To ensure that the samples for posterior analysis drawn after the sampler had reached convergence, the first 100,000 were discarded.

RESULTS

Mean and standard deviation of FP pecks and FP bouts are shown in Table 1. After generation 1, mean number of pecks and bouts were consistently larger in line HP compared with line LP. In generation 5, bout number and peck number were 3 times higher in line HP compared with line LP. In addition, the phenotypic mean of the 2 traits decreased gradually in line LP but fluctuated in line HP. The variation in bout number and peck number was

rather larger. The standard deviation was about 2.5 times the mean in the 2 traits, and there was a scale effect on standard deviation, i.e., standard deviation increased with an increase of mean.

Figure 1 (a, b) shows the skewness and kurtosis (expressed as absolute value) for the data transformed with different values of λ (range from -1 to 1). The transformation with $\lambda = -1$ gave a minimal skewness for number of FP bouts and number of FP pecks in line LP, but with $\lambda = -0.4$ in line HP. The transformation with $\lambda = -0.2$ gave an optimal kurtosis for number of FP bouts and with $\lambda = 0$ for number of FP pecks in both 2 lines. The $-2 \log$ maximum likelihood from REML analysis based on the given model is plotted in Figure 1c. The largest maximum likelihood (smallest $-2 \log$ maximum likelihood) was obtained from the data transformed using $\lambda = -0.2$ except for FP pecks in line LP, which had the largest maximum likelihood from the data transformed with $\lambda = -0.5$.

As a compromise between minimizing skewness and kurtosis and maximizing likelihood as well as performing a transformation as consistent among the traits and lines as possible, $\lambda = -0.2$ was chosen as the approximate optimal value to be used in the Box-Cox transformation for FP bouts and FP pecks in both lines. Table 2 shows the mean and standard deviation of bout number and peck number in the first generation and over all generations, based on the data using the Box-Cox transformation with $\lambda = -0.2$. In the first generation, bout number and peck number in the transformed scale were similar in the 2 lines. However, averaged over generations, bout number and peck number in line HP were about 1.5 times as high as in line LP. The standard deviations for the 2 traits in line LP were smaller than those in line HP, but the coefficients of variation in line LP were a little larger than those in line HP.

Table 3 shows variance components for number of FP bouts and number of FP pecks in Box-Cox transformed scale with $\lambda = -0.2$, estimated from the mean of the marginal posterior distribution obtained from the Bayesian approach. The variance of observation pen and the variance of full-sib group were close to zero in both traits and in both lines. The residual and phenotypic variances in line HP were significantly larger than those in line LP for both traits. The additive genetic variances in line HP

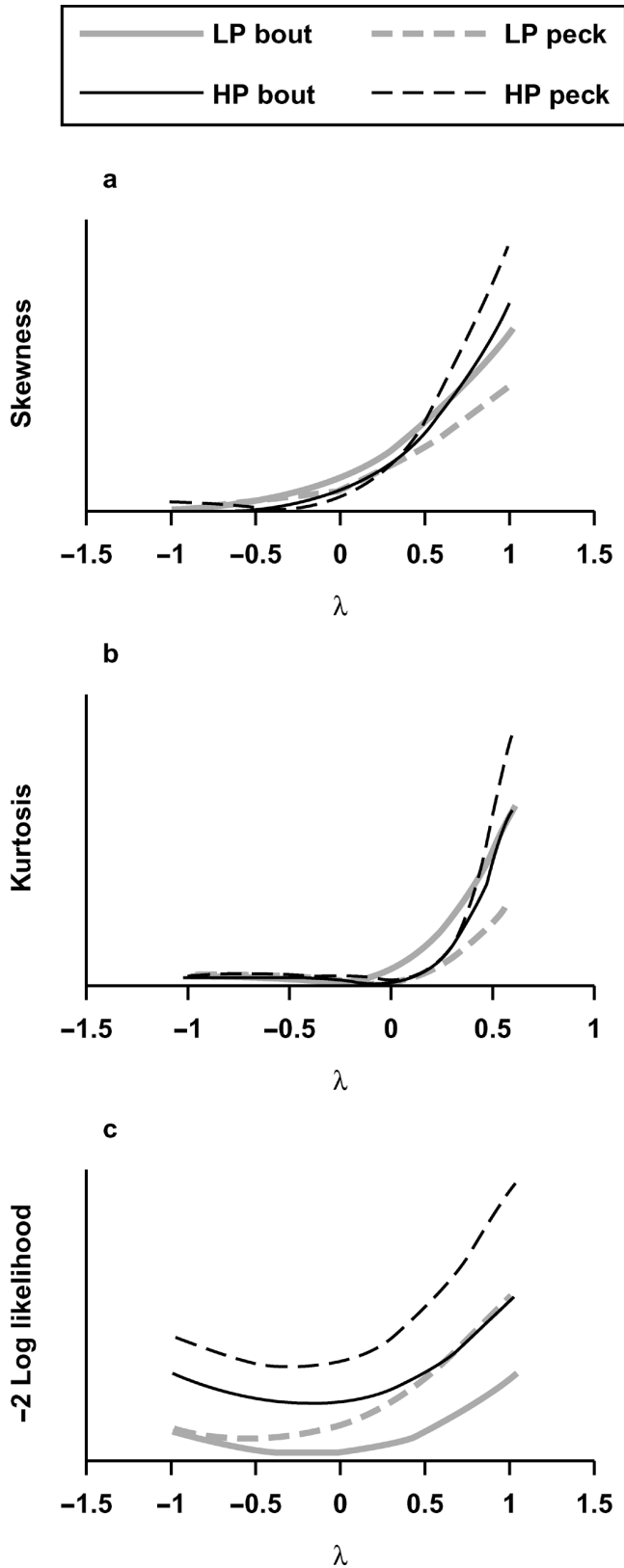


FIGURE 1. The skewness (a) and kurtosis (b) (expressed as absolute value) for the data transformed with different values of λ (ranging from -1 to 1), and the maximal likelihood (c) based on these transformations and the given model. LP bout = number of feather pecking bouts in the line selected for low feather pecking, LP peck = number of feather pecks in the line selected for low feather pecking, HP bout = number of feather pecking bouts in the line selected for high feather pecking, and HP peck = number of feather pecks in the line selected for high feather pecking.

tended to be larger than in line LP for FP bout but the difference was not statistically significant ($P = 0.345$). The h^2 for number of FP bouts was higher than that for number of FP pecks in both lines. The h^2 for the 2 traits were higher in line LP than in line HP. However, these differences between estimates of h^2 were not statistically significant.

The mean and standard deviation of the marginal posterior distribution of the additive genetic mean in each generation are shown in Table 4. In contrast with the phenotypic mean, the average breeding value changes smoothly over generations. In line LP, the average breeding value for number of FP bouts and number of FP pecks decreased linearly over generations, whereas the average breeding value increased linearly over generations in line HP. The regression (coefficient of regression \pm standard error) of average breeding value on the number of generations was -0.102 ± 0.003 and 0.125 ± 0.005 for number of FP bouts, and -0.128 ± 0.004 and 0.125 ± 0.003 for number of FP pecks in line LP and line HP, respectively.

Figure 2 shows the marginal posterior distribution of the total response measured as the difference between average breeding values in the last generation and the first generation. The distribution was approximately normal with slight negative skew in line LP and slight positive skew in line HP. Based on the mean of the marginal posterior distribution, over 4 generations of selection for number of FP bouts, the total response for this trait was -0.406 in line LP and 0.490 in line HP, and the total response for number of FP peck was -0.507 in line LP and 0.452 in line HP. In percentage of the mean of the first generation, the total response was 58% for number of FP bouts and 47% for number of FP pecks in line LP, and 74 and 46% in line HP, respectively.

The response in original scale (Figure 3) was approximately estimated by the inverse transformation from the generation mean of breeding values in transformed scale. Although the response in the transformed scale was nearly symmetric in the 2 lines, the response in original scale was rather asymmetric. Total response for number of FP bouts (1.663) in line HP was 2 times as large as that (-0.772) in line LP. Total response for number of FP pecks (2.469) in line HP was nearly 2 times as large as that (-1.516) in line LP.

DISCUSSION

Although the 2 lines were derived from the same base population, the data from each line were analyzed separately. The reason for this was that after one generation of selection there was consistently a large difference between the 2 lines with regard to performance and variation of FP. Furthermore, there seemed to be an interaction between line and environment as reflected by a larger fluctuation of mean performance among generations in line HP, whereas a relatively smooth change was seen in line LP. Thus, selection response was estimated without any reference to a control line. However, the methods based on animal models can effectively partition genetic

TABLE 2. Means and SD of number of feather pecks (FP peck) and number of feather pecking bouts (FP bout) in Box-Cox transformed scale with $\lambda = -0.2$ for the line selected for low feather pecking (LP) and the line selected for high feather pecking (HP) in the first generation and over generations

Generation	Line LP				Line HP			
	FP peck		FP bout		FP peck		FP bout	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
First generation	1.07	0.99	0.70	0.68	0.99	0.93	0.66	0.66
Over generations	0.85	0.95	0.57	0.65	1.28	1.09	0.92	0.83

changes from nongenetic changes without the need for control lines assuming that the model is correct (Sorensen and Kennedy, 1986). Therefore, the present analysis was carried out for each line and based on an animal model.

Genetic parameters are usually estimated by a linear model in which the dependent variables and the random effects are assumed to be normally distributed. When the distribution of the data departs far from a normal distribution, data transformation is often applied to make data close to normality to fulfill the model assumptions. In the current study, data were transformed using Box-Cox transformation with $\lambda = -0.2$. It was taken as an approximate optimal transformation with regard to maximum likelihood and normality. The genetic parameters and selection responses estimated based on this transformation were expected to be more reliable than those estimated on original data.

In the present study, variance components and breeding values were estimated using a Bayesian approach. In the Bayesian analysis, all parameters in the model were estimated simultaneously. Thus the estimates of breeding values and selection response accounted for the uncertainty associated with all other parameters in the model. In addition, the standard error of selection response could be obtained directly from the standard deviation of the marginal posterior distribution of the selection response.

The full-sib group effect in the model was expected to account for full-sib intraclass correlation caused by factors other than additive genetic effects. In the current study, the variance of this component appeared to be zero. It indicates that dominant and maternal effects as well as the environmental effect common to full-sibs were negligible for number of FP bouts and number of FP pecks. This is a very important result in relation to commercial

selection programs, as these programs normally involve several line crosses for the production of the commercially available hybrid (Besbes and Ducrocq, 2003).

It has been suggested that FP may spread by social transmission in groups of laying hen chicks (Zeltner et al., 2000). The present analysis took observing pen as a random effect into the model to account for environmental effect common to the birds in the same observing pen, which was expected to cover the effect of social transmission. However, no effect of observing pen could be found. This indicated that the effect of social transmission is very small in relation to genetic effects. Alternatively, the effect of social transmission was too small to be detected in the current data by the present method. It may be due to the fact that the birds were too old and stayed in the observing pen for too short a period to modify their feather-pecking behavior by seeing the other birds performing feather pecking.

Heritability for individual performance of FP has been reported in few previous studies. Cuthbertson (1980) estimated an h^2 of 0.56 using the data from 250 chickens, which were chosen out of 504 chickens and classified as peckers, but an h^2 of 0.09 using the data from all 504 chickens including nonclassified birds. Bessei (1984) showed an h^2 of 0.07 for frequency of FP at 8 to 18 wk of age. Kjaer and Sørensen (1997) investigated FP behavior in a purebred White Leghorn line and estimated h^2 of number of FP pecks to be 0.06, 0.14, and 0.38, and h^2 of number of FP bouts to be 0.13, 0.13, and 0.35 at 6, 38, and 69 wk of age, respectively. Rodenburg et al. (2003) classified FP as gentle when the recipient showed no reaction and the neck of the performer was still. Severe FP resulted in a reaction of the recipient and movement of the neck of the performer. These authors reported an

TABLE 3. The mean and SD of the marginal posterior distribution for phenotypic variance (σ_p^2), the ratios of variance for pen effect (c^2) and full-sib group effect (f^2), and heritability (h^2) of bout number and peck number in Box-Cox transformed scale with $\lambda = -0.2$

Trait ¹	Line ²	σ_p^2		c^2		f^2		h^2	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
FP bout	LP	0.435	0.022	0.001	0.003	0.000	0.000	0.174	0.069
	HP	0.717	0.036	0.000	0.000	0.001	0.005	0.139	0.065
FP peck	LP	0.892	0.044	0.000	0.000	0.000	0.000	0.139	0.056
	HP	1.223	0.059	0.000	0.000	0.000	0.000	0.105	0.054

¹FP bout = number of feather pecking bouts; FP peck = number of feather pecks.

²LP = the line selected for low feather pecking; HP = the line selected for high feather pecking.

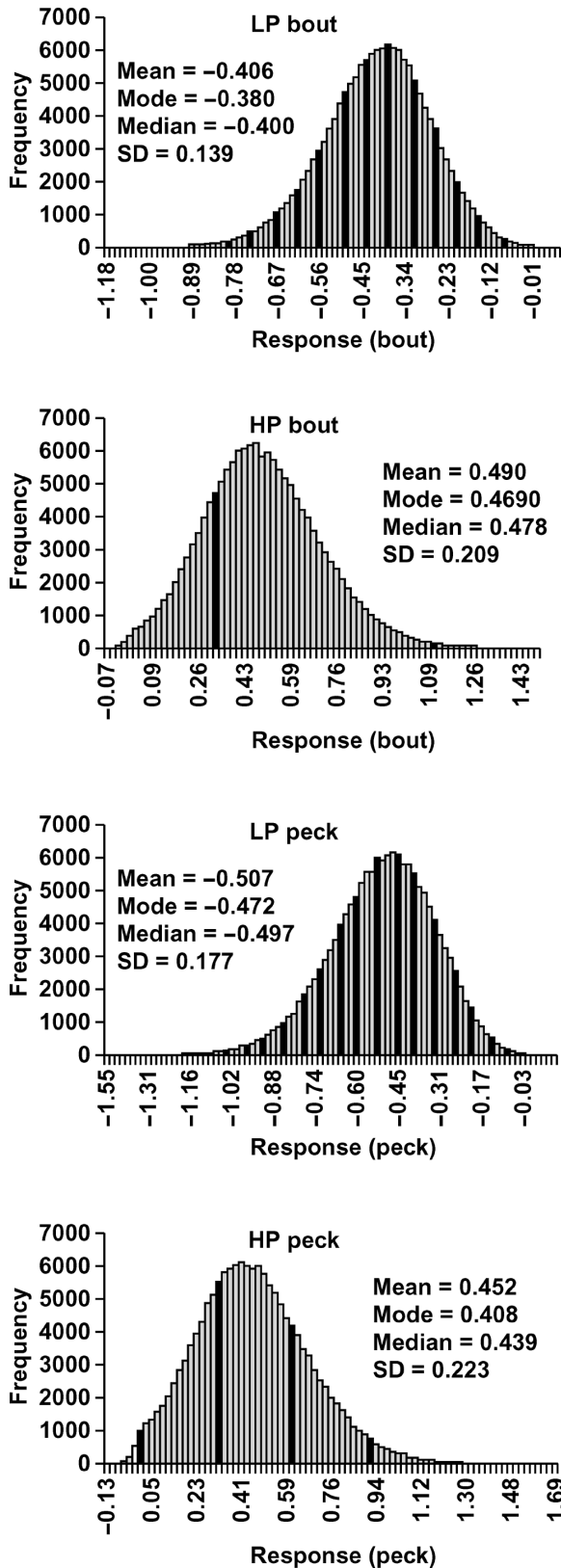


FIGURE 2. Histograms with mean, mode, median, and SD of marginal posterior distributions for total additive genetic gain. LP bout = number of feather pecking bouts in the line selected for low feather pecking, LP peck = number of feather pecks in the line selected for low feather pecking, HP bout = number of feather pecking bouts in the line selected for high feather pecking, and HP peck = number of feather pecks in the line selected for high feather pecking.

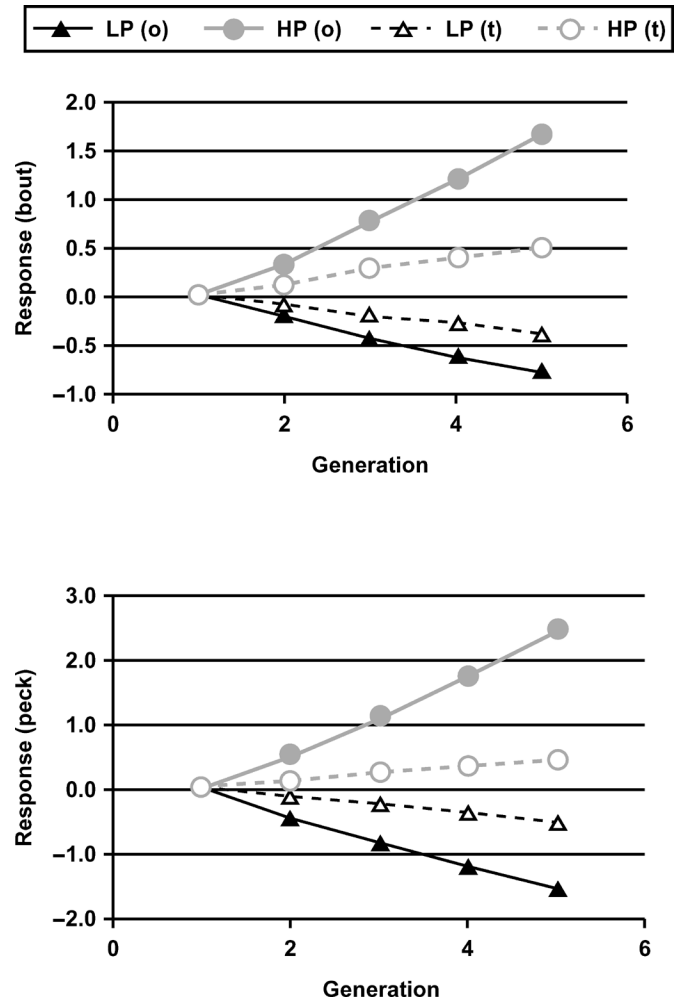


FIGURE 3. Response to selection in original scale and in Box-Cox transformed scale for number of feather pecking bouts and number of feather pecks. LP(o) = original scale in the line selected for low feather pecking, LP(t) = transformed scale in the line selected for low feather pecking, HP(o) = original scale in the line selected for high feather pecking, and HP(t) = transformed scale in the line selected for high feather pecking.

h^2 of 0.12, 0.08, 0.00, and 0.02 for number of gentle FP bouts, gentle FP pecks, severe feather pecking bouts, and severe FP pecks, respectively, at 6 wk of age; h^2 for these traits were 0.15, 0.16, 0.06, and 0.07, respectively, at 30 wk of age. In the present study, the FP behavior of the hens was recorded at about 30 wk. The estimates of heritability were 0.17 and 0.14 for number of FP bouts, and 0.14 and 0.11 for number of FP pecks in line LP and HP, respectively. These estimates were in agreement with these previous studies.

In the present experiment, selection was based on number of FP bouts at approximately 30 wk. Number of FP bouts, instead of number of FP pecks, was chosen as the selection criterion, considering that selection for number of FP pecks in line HP could be favorable for the hens doing gentle pecking. As observed, the frequency of FP pecks in each FP bout in the case of gentle pecking was much higher than that in severe pecking. The present study showed that the h^2 for number of FP bouts was

TABLE 4. The mean and SD of the marginal posterior distribution of average breeding values of each generation for number of feather pecking bouts (FP bout) and number of feather pecks (FP peck) in Box-Cox transformed scale with $\lambda = -0.2$ for the line selected for low feather pecking (LP) and the line selected for high feather pecking (HP)

Generation	Line LP				Line HP			
	FP bout		FP peck		FP bout		FP peck	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	-0.022	0.069	-0.019	0.089	0.011	0.076	0.000	0.089
2	-0.107	0.085	-0.126	0.111	0.133	0.107	0.126	0.124
3	-0.214	0.107	-0.253	0.137	0.283	0.150	0.248	0.165
4	-0.310	0.131	-0.387	0.168	0.399	0.192	0.351	0.204
5	-0.428	0.151	-0.526	0.193	0.501	0.222	0.453	0.236

higher than that for number of FP pecks. The results indicated that it is an advantage to use number of FP bouts as a selection trait.

In spite of moderately low h^2 , selection for FP was still very effective due to large variation. Although h^2 for number of FP bouts in line HP was lower than that in line LP, line HP showed a larger response in this trait, probably due to a larger genetic variation in line HP. On the other hand, line LP got a larger response for FP pecks than line HP. A possible explanation is that h^2 for number of FP pecks in line LP was higher than that in line HP, although additive genetic variances for number of FP pecks were similar in the 2 lines. As a whole, the response in the transformed scale was nearly symmetrical in the 2 lines, but it should be kept in mind that responses to divergent selections in a Box-Cox transformed scale are not necessarily symmetrical. On the other hand, in original scale, total response in line HP was much larger than that in line LP for number of LP bouts and number of FP pecks. This can be explained by the fact that the distribution of the data was negatively skewed.

In conclusion, estimates of genetic parameters for FP behavior in laying hens based on the longest selection history and largest data set available to date were presented. Results from the current study showed there was a large phenotypic and genetic variation for FP within strain. Heritability for feather pecking behavior was low or moderate with higher h^2 for number of FP bouts and lower h^2 for number of FP pecks. Even though h^2 was not high, selection for and against FP resulted in a large genetic change in FP behavior due to the large variation within strain. No full-sib effect could be detected, indicating that dominant and maternal effects were small. No variation between observation pens could be found; implying that social transmission of FP behavior for adult hens during a settling period of 7 to 12 d was negligible. The variance components and the actual selection response together suggest that genetic selection could be a useful tool in minimizing FP behavior in commercial stocks of laying hens. This would be expected to reduce one of the major welfare problems in egg production.

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