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Estimation of heritability and genetic correlation of body weight gain and growth curve parameters in Korean native chicken

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Objective: This study estimated the genetic parameters for body weight gain and growth curve parameter traits in Korean native chicken (KNC).
Methods: A total of 585 F_1 chickens were used along with 88 of their F_0 birds. Body weights were measured every 2 weeks from hatching to 20 weeks of age to measure weight gain at 2-week intervals. For each individual, a logistic growth curve model was fitted to the longitudinal growth dataset to obtain three growth curve parameters (α, asymptotic final body weight; β, inflection point; and γ, constant scale that was proportional to the overall growth rate). Genetic parameters were estimated based on the linear-mixed model using a restricted maximum likelihood method.
Results: Heritability estimates of body weight gain traits were low to high (0.057 to 0.458). Heritability estimates for α, β, and γ were 0.211±0.08, 0.249±0.09, and 0.095±0.06, respectively. Both genetic and phenotypic correlations between weight gain traits ranged from –0.527 to 0.993. Genetic and phenotypic correlation between the growth curve parameters and weight gain traits ranged from –0.968 to 0.987.
Conclusion: Based on the results of this study population, we suggest that the KNC could be used for selective breeding between 6 and 8 weeks of age to enhance the overall genetic improvement of growth traits. After validation of these results in independent studies, these findings will be useful for further optimization of breeding programs for KNC.

Keywords: Korean Native Chicken; Logistic Model; Selection; Genetic Parameter; Breeding

INTRODUCTION

Chicken is one of the most popular poultry species and it accounts for 86.4% of the consumption of poultry meat worldwide because of rapid development in the broiler industry over the last 50 years [1]. There are numerous indigenous chicken breeds and their economic traits and genetic potential remain largely unknown. Recently, much attention has been focused on indigenous chickens as meat or layer strains because of increasing consumer demand and environmentally viable characteristics of local ecotypes.

Elucidation of changes in chicken growth trajectory over time under a given management system is important for the improvement of poultry meat production. In fact, growth curves have been widely used to describe poultry growth trajectories and summarize it using a few biologically meaningful parameters [2-4]. Knowledge of growth curve parameters is used to determine the age at which to select birds and to design management procedures for breeding programs [5]. The use of body weight at a given time as selection criteria in breeding program and estimations for heritability of growth curve parameters for chicken has been reported previously [6-8]. Thus, they can provide a sound biological basis for designing a breeding program which improves productivity, efficiency, and capability throughout the entire growth period [9].

Korean native chicken (KNC) population was established and maintained by the National Institute of Animal Science, Republic of Korea. As the result of project named "Restoration of Korean native chicken" launched in 1994 and the subsequent selective breeding program, five distinct chicken lines, based on their plumage color, were established: Heuk-saek Jaerae-Jong (black), Hoegalsaek Jaerae-jong (gray brown), Jeokgalsaek Jaerae-jong (red brown), Baeksaek Jaerae-jong (white), and Hwanggalsaek Jaerae-jong (yellow brown) [10]. Although KNCs have a unique meat flavor and superior nutrition content compared to commercial broilers [11], retarded growth performance and high variation in body weight are obstacles for their commercialization [12]. However, moderate to high heritabilities of body weight traits have been reported for KNC [13].

The objective of present study was to provide estimates of the genetic parameters of weight gain, growth curve parameters (*i.e.*, α, asymptotic final body weight; β, inflection point at which 50% of the asymptotic body weight is realized; γ, constant scale that is proportional to the overall growth rate) in KNC.

MATERIALS AND METHODS

Animal care
All the practices and procedures in this study were strictly followed "The Guide for Care and Use of Laboratory Animals" published by the Institutional Animal Care and Use Committee of NIAS, Korea.

Animals
The experimental animals included the F_0 and F_1 generations of KNC resource pedigree. The KNC nuclear pedigree consisted of 83 F_0 founders (15 males and 68 females) and 585 F_1 progeny (282 males, 303 females). Within-line mating was practiced in which a total of three cockerels were mated with 4 to 5 hens to produce F_1 birds. The F_1 progeny from two batches were categorized into the five lines: Red brown (R) (n = 135), White (W) (n = 122), Yellow brown (Y) (n = 130), Gray brown (G) (n = 110), Black (L) (n = 88) based on their plumage color. This resource population be made of 68 full-sib families with 3 to 20 birds (average 10.6). With regard to half-sib families, the population was consisted of 15 half-sib families ranging from 28 to 59 birds (average 44.5). Dams were not used for hatching and brooding. All animals were nurtured under standard breeding and management procedures implemented by the National Institute of Animal Science (NIAS) of Korea. The same environmental and feeding regime was provided throughout the experimental period of 20 weeks.

Growth data collection
Body weight traits were measured as a part of the breeding and maintenance procedures. For each bird, body weight at a specific age was recorded from hatching to 20 weeks of age at 2-week intervals. Body weight gain during each 2-week period was obtained from hatching to 20 weeks of age. (i.e., weight gain from hatch to 2 weeks of age [GR0-2], weight gain from 2 to 4 weeks of age [GR2-4], weight gain from 4 to 6 weeks of age [GR4-6], weight gain from 6 to 8 weeks of age [GR6-8], weight gain from 8 to 10 weeks of age [GR8-10] and so forth). The normality of body weight data and body weight gain traits were ascertained. If putative outliers were identified, they were excluded based on the Ryan-Joiner method, which was executed in Minitab software [14].

Growth curve data analysis
For the KNC population, parameters of growth curves were estimated using Gompertz, von Bertalanffy, and logistic growth curve functions in the SAS NLIN procedure [15]. To determine the fit of the growth curves, an R^2 value was computed by using the SAS NLIN procedure. In addition, convergence properties (*i.e.*, number of chickens that the model did not converge) and convergence weight (*i.e.*, number of chickens for which the converged weight at 20 weeks of age was 5 times heavier than their actual weight) were used as criteria for the fit of growth curves. These two criteria were obtained using Minitab's programming language [14]. Equations for the three growth curve models are given in Table 1. For each individual KNC, three parameters (*i.e.* α, asymptotic live body weight, β, inflection point at which 50% of the asymptotic weight is realized; and γ, a constant scale that is proportional to the overall growth rate) from the best-fit equation were extracted using Minitab's programming language.

Genetic parameter estimation
Fixed effect of sex, line, and batch were tested for significance in each trait in a general linear model using Minitab statistical software [14]. The (co)variance components and heritability for all traits were estimated with the following univariate linear mixed-effects model using the ASReml program [16].

Y = Xb+Za+e

Where, **Y** is a vector corresponds to the phenotypic values for weight gain traits and growth curve parameter traits; **b** is the vector of fixed effects including batch, lines, sex, and; **a** is a vector of random additive genetic effects, assumed to be **a**~ N (0, **A** σ_a^2);

Table 1. Equations for modeling the growth of Korean native chicken

Model	Equation
Gompertz	$W_{(t)} = \alpha e^{-\beta e^{-\gamma t}}$
von Bertalanffy	$W_{(t)} = \alpha (1 - \beta e^{-\gamma t})^3$
Logistic	$W_{(t)} = \alpha /(1 + \beta e^{-\gamma t})$

$W_{(t)}$ is the corresponding weight at time t; α, asymptotic live body weight (gram); β, the log-function for the proportion of the asymptotic mature weight to be gain after birth (wk); γ, a constant scale that is proportional to the overall growth rate (wk).

A is considered as additive genetic relationship matrix obtained from the nuclear F_1 pedigree and σ_a^2 is the additive genetic variance; **e** is a vector of random residual effects assumed to be **e**~ N $(0, I\sigma_a^2)$; **I** is the identity matrix and σ_a^2 is the residual variance; and **X** and **Z** are incidence matrices related to fixed and random effects, respectively.

Genetic correlation coefficients were estimated by the following bivariate linear mixed-effects model using ASReml [16]:

$$\begin{bmatrix} \mathbf{y_1} \\ \mathbf{y_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{X_2} \end{bmatrix} \begin{bmatrix} \mathbf{b_1} \\ \mathbf{b_2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z_2} \end{bmatrix} \begin{bmatrix} \mathbf{a_1} \\ \mathbf{a_2} \end{bmatrix} + \begin{bmatrix} \mathbf{e_1} \\ \mathbf{e_2} \end{bmatrix}$$

Where, $\mathbf{y_1}$ and $\mathbf{y_2}$ are vectors of measured phenotypes for the two traits under consideration; $\mathbf{b_1}$ and $\mathbf{b_2}$ are vectors of fixed effects (*i.e.*, sex, batch, and line) for the traits; $\mathbf{a_1}$ and $\mathbf{a_2}$ are vectors of the random additive genetic effects for the traits; $\mathbf{X_1}$ and $\mathbf{X_2}$ are the incidence matrices relating measures of the traits to fixed effects; $\mathbf{Z_1}$ and $\mathbf{Z_2}$ are the incidence matrices relating phenotypic observations with random additive genetic effects; and $\mathbf{e_1}$ and $\mathbf{e_2}$ are vectors of random residuals. The expectation and variance of the bivariate model were:

$$E \begin{bmatrix} \mathbf{y_1} \\ \mathbf{y_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{X_2} \end{bmatrix} \begin{bmatrix} \mathbf{b_1} \\ \mathbf{b_2} \end{bmatrix}$$

And

$$Var \begin{bmatrix} \mathbf{a_1} \\ \mathbf{a_2} \\ \mathbf{e_1} \\ \mathbf{e_1} \end{bmatrix} = \begin{bmatrix} A\sigma_{a11}^2 & A\sigma_{a12}^2 & 0 & 0 \\ A\sigma_{a21}^2 & A\sigma_{a22}^2 & 0 & 0 \\ 0 & 0 & I\sigma_{e11}^2 & I\sigma_{e12}^2 \\ 0 & 0 & I\sigma_{e21}^2 & I\sigma_{e22}^2 \end{bmatrix}$$

Where, **A**: the additive genetic relationship matrix; σ_{a11}^2, σ_{a12}^2, σ_{a21}^2, σ_{a22}^2 are additive genetic (co)variances for the traits under consideration; σ_{e11}^2, σ_{e12}^2, σ_{e21}^2, σ_{e22}^2 are residual (co)variances for the traits; and **I** is the identity matrix. **a** and **e** were assumed to be normally distributed with zero mean and (co)variances, as stated above. Phenotypic correlation coefficients were computed using the Minitab program [14].

RESULTS

Growth curve determination and descriptive statistics

We evaluated three widely used growth curve models (*i.e.*, Gompertz, von Bertalanffy, and logistic models) to fit the growth curve of the KNC population from hatching to 20 weeks of age (Table 2). In terms of R^2 values, the three models performed similarly in fitting the growth curve of KNCs. However, the logistic curves showed the best performance both in the convergence properties and the convergence weight (Table 2). Thus, the logistic model chose to conduct the subsequent analyses. The descriptive statistics of the growth curve parameter values (*i.e.*, the asymptotic live body weight α [grams], the scaling parameter β [wk], and the intrinsic growth rate γ [wk]) estimated from the logistic growth curve function are summarized in Table 3. The growth curves of KNC individuals were plotted from actual longitudinal body weight data from hatching to 20 weeks of age (Supplementary Figure S1).

Heritability estimates of weight gain and growth curve parameters

Table 4 shows the heritability estimates of weight gain and growth curve parameter traits in KNC. The heritability estimates of GR0-2 were high with estimates of 0.458, whereas GR2-4 and GR6-8 were moderate with estimates of 0.266 and 0.233 respectively. The heritabilities of GR4-6, GR8-10, and GR10-12 were low with heritability estimates of 0.161, 0.088, and 0.058 respectively. Heritability estimates of GR16-18 and GR18-20 were comparable with the value for GR10-12. Moderate heritability for growth curve parameter traits α and β were observed with estimates of 0.211 and 0.249, respectively. The heritability estimate for γ was low (0.095).

Table 3. Descriptive analysis of growth curve parameter related traits (α, β, γ)

Trait	N	Mean	SE	Min.	Max.
UT					
α (g)	557	2,180.20	22.4	1,111.70	4,653.10
β (wk)	560	19.52	0.34	8.79	53.82
γ (wk)	567	0.23	0.01	0.14	0.35
NLT					
α (g)	567	7.66	0.01	7.01	8.44
β (wk)	560	2.90	0.02	2.17	3.99

UT, untransformed data; α, asymptotic live body weight (g); β, inflection point at which 50% of the asymptotic weight is realized (wk); NLT, natural log transformed values; the inflection point age at t_i and weight W(t_i) are given by log_e(β)/α and α/2, respectively.

Table 2. Estimated parameters of growth curve using three non-linear models in Korean native chicken

Model	Parameter			R^2	Convergence property	Convergence weight
	α±SE (g)	β±SE (wk)	γ±SE (wk)			
Gompertz	2,798.9 ± 76.2	3.562 ± 0.04	0.102 ± 0.003	99.55	2	48
von Bertalanffy	3,755.4 ± 168.7	0.750 ± 0.00	0.061 ± 0.003	99.57	30	138
Logistic	2,076.3 ± 27.5	16.09 ± 0.41	0.222 ± 0.004	99.45	1	3

α, asymptotic live body weight (g); β, the log-function for the proportion of the asymptotic mature weight to be gain after birth (wk); γ, constant scale that is proportional to the overall growth rate (wk); R^2 is the coefficient of determination; Convergence properties can be defined as the number of chickens which the model is not converged; Convergence weight can be defined as the number of chickens for which the converged weight at 20 weeks of age is 5 times heavier than actual weight.

Table 4. Number of animals, mean and standard deviation, and heritability estimates for weight gain and growth curve parameter traits of Korean native chicken

Trait[1]	n	Mean±SD	V_a	V_e	h^2±SE
GR0-2	578	105.36±23.49	102.77	121.68	0.458±0.117
GR2-4	584	122.88±48.84	179.90	497.08	0.266±0.098
GR4-6	584	161.22±66.29	164.87	859.48	0.161±0.078
GR6-8	583	180.44±71.82	406.03	1,334.34	0.233±0.090
GR8-10	581	160.32±69.04	352.10	3,667.61	0.088±0.058
GR10-12	582	223.75±93.35	336.88	5,453.45	0.058±0.056
GR12-14	582	188.05±90.38	246.74	5,626.51	0.042±0.046
GR14-16	576	209.20±77.20	584.16	3,964.95	0.128±0.067
GR16-18	582	206.44±109.64	326.57	4,537.18	0.067±0.050
GR18-20	583	191.15±72.89	258.98	4,314.20	0.057±0.052
α	575	2,178.9±528.1	0.005	0.019	0.211±0.084
β	568	19.49±8.09	0.010	0.029	0.249±0.091
γ	565	0.230±0.032	6.16e-05	5.84e-04	0.095±0.060

n, number of animals analyzed; Mean±SD, mean with standard deviation; V_a, additive genetic component; V_e, residual variance component; h^2±SE, heritability with standard error.
[1] GR0-2, weight gain from hatch to 2 weeks of age; GR2-4, weight gain from 2 to 4 weeks of age; GR4-6, weight gain from 4 to 6 weeks of age; GR6-8, weight gain from 6 to 8 weeks of age; GR8-10, weight gain from 8 to 10 weeks of age; GR10-12, weight gain from 10 to 12 weeks of age; GR12-14, weight gain from 12 to 14 weeks of age; GR14-16, weight gain from 14 to 16 weeks of age; GR16-18, weight gain from 16 to 18 weeks of age; GR18-20, weight gain from 18 to 20 weeks of age; α, asymptotic live body weight (gram); β, inflection point at which 50% of the asymptotic weight is realized (wk), γ, a constant scale that is proportional to the overall growth rate (wk).

Genetic and phenotypic correlations

Table 5 describe genetic and phenotypic correlation coefficients that were estimated from the growth curve parameters and weight gain traits. Most of the genetic correlation coefficients among the growth curve parameters and weight gain traits were higher compared to those for the phenotypic parameter correlation. The range of coefficients was between –0.968 and 0.993. The genetic correlations between early weight gain traits were high and positive, whereas it becomes low and negative at later weight gain. Genetic correlations between α and weight gain traits from GR10-12 to GR 18-20 were strong and positive. Similarly, genetic correlations between β and weight gain traits from GR10-12 to GR18-20 were positive and ranged between 0.214 to 0.723. Correlation results between growth curve parameters are shown in Table 5. Genetic and phenotypic correlations between α and β were strong and positive (0.582 and 0.696, respectively). Negative phenotypic and genetic correlations were observed between β and γ (–0.264 and –0.370, respectively). Negative genetic and phenotypic correlations between α and γ were recorded.

DISCUSSION

Growth can be characterized by size increment or gain at a given age or from an initial size. Therefore, weight gain can be defined as the difference between measurement at the beginning and end of the time interval. In our study, we measured body weight

Table 5. Genetic (above the diagonal), phenotypic (below the diagonal) correlation between weight gain traits and parameters of the growth curve (GR0-2 to GR18-20, α, β, γ)[1]

Trait[2]	GR0-2	GR2-4	GR4-6	GR6-8	GR8-10	GR10-12	GR12-14	GR14-16	GR16-18	GR18-20	α	β	γ
GR0-2	-	0.434	0.723	0.545	0.615	0.717	–0.258	–0.140	0.050	0.130	0.063	–0.667	0.198
GR2-4	0.808	-	0.742	0.550	0.502	0.706	0.295	–0.300	–0.527	–0.241	–0.298	–0.657	0.654
GR4-6	0.754	0.812	-	0.920	0.652	0.939	0.993	0.270	0.611	–0.517	0.177	–0.393	0.540
GR6-8	0.743	0.777	0.799	-	0.417	0.971	0.083	0.208	0.198	–0.228	0.288	–0.264	0.987
GR8-10	0.213	0.224	0.216	0.208	-	0.981	0.507	0.143	0.329	–0.235	–0.277	–0.485	0.671
GR10-12	0.401	0.456	0.498	0.504	–0.011	-	0.730	0.605	0.416	–0.385	0.687	0.214	0.542
GR12-14	–0.05	–0.03	–0.024	0.002	0.190	0.079	-	0.780	0.850	–0.277	0.936	-	0.183
GR14-16	0.188	0.192	0.244	0.220	0.280	0.224	0.228	-	0.888	–0.271	0.772	0.369	–0.210
GR16-18	–0.298	–0.314	–0.365	–0.371	0.223	–0.060	0.367	0.194	-	0.021	0.930	0.723	–0.543
GR18-20	0.115	0.021	0.099	0.099	0.091	0.140	0.150	0.193	0.190	-	0.584	0.311	–0.968
α	0.399	0.463	0.576	0.581	0.251	0.483	0.031	0.014	0.550	–0.335	-	0.528	–0.388
β	–0.590	–0.665	–0.624	–0.569	0.096	–0.071	0.475	0.231	0.649	0.190	0.696	-	–0.370
γ	0.073	0.021	0.006	0.005	0.297	0.219	0.544	0.542	0.711	0.514	–0.560	–0.264	-

[1] Genetic correlations are above the diagonal and phenotypic correlations are below the diagonal, Traits: weight gain traits and growth curve parameter traits.
[2] GR0-2, weight gain from hatch to 2 weeks of age; GR2-4, weight gain from 2 to 4 weeks of age; GR4-6, weight gain from 4 to 6 weeks of age; GR6-8, weight gain from 6 to 8 weeks of age; GR8-10, weight gain from 8 to 10 weeks of age; GR10-12, weight gain from 10 to 12 weeks of age; GR12-14, weight gain from 12 to 14 weeks of age; GR14-16, weight gain from 14 to 16 weeks of age; GR16-18, weight gain from 16 to 18 weeks of age; GR18-20, weight gain from 18 to 20 weeks of age; α, asymptotic live body weight (g); β, inflection point at which 50% of the asymptotic weight is realized (wk); γ, constant scale that is proportional to the overall growth rate (wk).

gain at 2-week intervals until 20 weeks of age. Similar to Aslam et al [5] and Ngeno et al [17], we considered three growth curve parameters (*i.e.*, α, β, and γ) as a single trait to estimate genetic parameters in the moderate sized KNC population. In terms of the convergence property and weight, the logistic model described the growth pattern of KNC better than did the other two models (Table 1). Thus, the logistic growth curve function was selected to estimate growth curve parameters for further analyses.

Heritability estimates for body weight of our study population were reported by Cahyadi et al [13] and were in agreement with those reported in previous studies [18-21]. Furthermore, the estimated heritability values for body weight gain traits were lower than those reported for body weight traits. The highest heritability estimate for weight gain was exhibited at GR0-2 weeks. The trend in heritability observed for weight gain for this KNC population was similar to that reported for body weight in previous studies. Heritability estimates for body weight related traits exhibited a decreasing trend with increasing age in the KNC population. Similar results were observed by Adeyinka et al [22] and Saatchi et al [23]. The α (asymptotic mature weight) showed a moderate heritability that was inconsistent with the results of Mignon-Grasteau et al [7], Aslam et al [5], and Narinc et al [24]. The moderate heritability for α indicated that some genetic gain through selection could be achieved. In addition, we found that the low heritability estimates for β and γ were consistent with the results of Aslam et al [5] and Narinc et al [24] for turkey and Japanese quail, respectively.

Akbas and Yaylak [25] reported that birds with high α values had high hatch weights. However, we observed only a moderate level of genetic correlation between GR0-2 and α. The genetic correlations between body weight gain and β had different signs and/or magnitude. Strong negative genetic and phenotypic correlations were observed for GR0-2 to GR8-10, which become positive at later stages of growth, similar to that reported by Barbato [26] in mice and Mignon-Grasteau et al [7] in chickens.

The positive correlation between α and β was in agreement with correlation estimates reported for Japanese quail growth using the Gompertz model [24]. These results indicate that individuals with high asymptotic body weight will longer to reach β. The parameters β and γ exhibited moderate negative phenotypic and genetic correlation in contrast with Aslam et al [5], where they obtained a positive correlation (0.64) between these parameters in turkey. The genetic correlation between α and γ was –0.388, whereas the phenotypic correlation was –0.560. The negative correlation between α and scaled γ indicated that if selection was used to increase asymptotic body weight there would be a negative effect on the scaling parameter γ.

Heritability estimates of weight gain of the KNC population were high and moderate during the juvenile stage and decreased with age. Previously we reported the genetic parameters using cross-sectionally measured body weight data (*e.g.* body weight at 6 weeks of age, body weight at 8 weeks of age) in KNC [13].

Compared to the previous study, we analyzed weight gain data given two-week of period (*e.g.*, GR6-8) in this study. As a result, we could clearly differentiate high or low heritability (Table 4). High heritabilities were observed from early stage of growth, which are likely to reflect genetic variability. On the contrary, low heritabilities were observed from late stage of growth, which are likely to reflect genetic invariability. For the genetic phenotypic correlation coefficients, analysis of weight gain data allowed us to detect both positive and negative signs which could not be seen the previous study [13]. The growth curve parameter was heritable with a low to moderate estimate, and low genetic and phenotypic correlation with weight gain, and consequently the alteration of the growth curve of KNC by selection.

The results of estimation of heritability suggest that the KNC could be used for selective breeding at juvenile stages, between 6 and 8 weeks of age, to increase the genetic improvement of growth performance traits. The heritability for the period between 6 and 8 weeks of age was not highest (Table 4). In fact, the period between 2 and 4 weeks of age showed maximum heritability. However, the standard deviation of the period between 6 and 8 weeks of age is larger than that of the period between 2 and 4 weeks of age (Table 4). Thus, given the selection intensity, we can anticipate the maximum expected genetic gain based on the individual selection at the period between 6 and 8 weeks of age. The findings of this study could provide useful information for further optimization of breeding plans for KNC after verification of these results in independent studies.

CONFLICT OF INTEREST

We certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

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