Genetic analysis of bone quality traits and growth in a random mating broiler population

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ABSTRACT We report the genetic relationship between growth and bone quality traits in a random mating broiler control population. Traits studied were growth rates from week 0 to 4 [body weight gain (BWG) 0 to 4], from week 0 to 6 (BWG 0 to 6), and residual feed intake (RFI) from week 5 to 6 (RFI 5 to 6). Bone quality traits were obtained at 6 weeks of age. These traits were shank weight (SW), shank length (SL), shank diameter (SDIAM), tibia weight (TW), tibia length (TL), and tibia diameter (TDIAM). Likewise, tibia was used to obtain the tibia density (TDEN), tibia breaking strength (TBS), tibia mineral density (TMD), tibia mineral content (TMC), and tibia ash content (TAC). At the phenotypic level, growth traits were positively correlated with most of the bone quality traits except with TDEN and TAC which tended to show unfavorable associations (−0.04 to −0.31). Heritability of bone quality traits ranged from 0.08 to 0.54. The additive genetic associations of growth traits with weight, length, and diameter of shank and tibia were positive (0.37 to 0.80). A similar pattern was observed with TMD and TMC (0.06 to 0.65). In contrast, growth traits showed unfavorable genetic associations with TDEN, TBS, and TAC (−0.03 to −0.18). It was concluded that bone quality traits have an additive genetic background and they can be improved by means of genetic tools. It appears that selection for growth is negatively correlated with some traits involved in the integrity, health, and maturity of leg bones.

Key words: bone quality, growth, residual feed intake

INTRODUCTION

The broiler chicken industry has improved growth to increase meat yield through genetic selection (Williams et al., 2004). Selection for growth has arguably resulted in growth rate from week 0 to 4 [body weight gain (BWG) 0 to 4], from week 0 to 6 (BWG 0 to 6), and residual feed intake (RFI) from week 5 to 6 (RFI 5 to 6). Bone quality traits were obtained at 6 weeks of age. These traits were shank weight (SW), shank length (SL), shank diameter (SDIAM), tibia weight (TW), tibia length (TL), and tibia diameter (TDIAM). Likewise, tibia was used to obtain the tibia density (TDEN), tibia breaking strength (TBS), tibia mineral density (TMD), tibia mineral content (TMC), and tibia ash content (TAC). At the phenotypic level, growth traits were positively correlated with most of the bone quality traits except with TDEN and TAC which tended to show unfavorable associations (−0.04 to −0.31). Heritability of bone quality traits ranged from 0.08 to 0.54. The additive genetic associations of growth traits with weight, length, and diameter of shank and tibia were positive (0.37 to 0.80). A similar pattern was observed with TMD and TMC (0.06 to 0.65). In contrast, growth traits showed unfavorable genetic associations with TDEN, TBS, and TAC (−0.03 to −0.18). It was concluded that bone quality traits have an additive genetic background and they can be improved by means of genetic tools. It appears that selection for growth is negatively correlated with some traits involved in the integrity, health, and maturity of leg bones.

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Femur, tibia, and shank constitute the main bones of the leg (Sharman et al., 2007), and their quantitative assessment for quality and integrity include bone breaking strength (BBS), mineralization level (Hester et al., 2004), and morphological variables (Rath et al., 2000). Bone strength is influenced by several different properties (Turner, 2002; Currey, 2003; Davidson et al., 2006; Seeman and Delmas, 2006) such as shape, size, mass, structure, and composition (McDevitt et al., 2006; Lewis et al., 2009; Shaw et al., 2010). Dual-energy x-ray absorptiometry (DXA) methodology has been used for rapid measurement of bone mineral content (BMC) and bone mineral density (BMD). While BMC is the measure of the minerals in the bone, BMD is a mathematical ratio of the BMC in a defined area of bone (Licata and Williams, 2014). However, given the body mass that legs have to support, bone morphological traits have been related to the propensity to leg problems (Deeb and Lamont, 2002). Studies in poultry show that, at phenotypic level, BBS is positively correlated with BMD, bone ash content (BAC), and bone weight (Frost and Roland, 1991; Rath et al., 1999; Yalcin et al., 2001). As a result, bone mineralization-related traits are often used as strength indices (Rath et al., 2000; Hester et al., 2004; Lewis et al., 2009). Recently, Shim et al. (2012) using BBS, BAC, and BMD...
as bone quality indicators observed that bone quality of slow growing broilers was better compared to the fast growing ones and further asserted that faster growing chickens were disadvantaged by the body weight they had to support.

There is a suggestion that bone mechanical properties could be alleviated through modulation of growth rate (Williams et al., 2000; Williams et al., 2004); however, a report by Leterrier et al. (1998) refutes such an approach. It has been shown that there is an additive genetic component that underlies bone quality in turkey (Havenstein et al., 1988) and laying hens (Bishop et al., 2000), but the genetic relationship between growth rate and leg skeletal integrity in meat-type chickens has not been sufficiently documented (Merritt, 1966; de Verdal et al., 2013) even though the inclusion of leg quality traits in broiler breeding programs has been described (Whitehead, 2007).

The objective of the current study was to analyze the genetic basis of skeletal integrity in broiler chickens and ascertain the genetic relationship, between growth rate and leg skeletal integrity and bone quality, in a random-bred broiler chicken population.

MATERIALS AND METHODS

Study Population and Husbandry

A data base of 2,301 pedigreed broiler chickens, produced in 8 consecutive hatches from mating 24 sires and 72 dams, was used in this study. The data were obtained using the Arkansas random mating population which is an unselected broiler control population (Aggrey et al., 2010). Once hatched, chicks were sexed and placed in pens (0.071 m²/bird) with litter. From hatching to 18 days the chickens received a mash starter diet containing 225 g/kg protein, 52.8 g/kg fat, 25.3 g/kg fiber, 12.90 MJ ME/kg, 9.5 g/kg calcium (Ca), and 7.2 g/kg total phosphorus (P) (4.5 g/kg available P). Henceforth chickens were fed a pelleted grower diet containing 205 g/kg protein, 57.6 g/kg fat, 25.0 g/kg fiber, 13.20 MJ ME/kg, 9.0 g/kg Ca, and 6.7 g/kg total P (4.1 g/kg available P). At 28 days of age, birds were transferred to individual metabolic cages (width = 20.32 cm, length = 60.96 cm, and height = 30.48 cm). They were allowed to acclimate for 1 week prior to measuring feed efficiency from 5 to 6 wk. Water and feed were provided ad libitum for the duration of the study. Birds were kept on a 20L:4D light regimen.

Data

Weekly body weight was recorded for each bird from hatch until 6 weeks, and feed intake was measured from week 5 to 6. Body weight gain (BWG), from week 0 to 4 (i.e., BWG 0 to 4) and from week 0 to 6 (BWG 0 to 6) was calculated. Residual feed intake (RFI) from week 5 to 6 (i.e., RFI 5 to 6) was computed according to Aggrey et al. (2010). At 6 weeks, chickens were killed by exsanguination, scalded, defeathered, and eviscerated. Carcasses were chilled on ice in a cooler at 5°C overnight. At the next day, carcasses were processed and both femurs were dislocated to remove the legs from the frame. In order to obtain morphological traits, shanks were measured for shank weight (SW), shank length (SL), and shank diameter (SDIAM). Values from both legs were averaged to obtain a single value for each trait. On the other hand, only right tibia was measured for tibia weight (TW), tibia length (TL), tibia diameter (TDIAM), and breaking strength tibia (TBS), and only left tibia was measured for tibia mineral density (TMD), tibia mineral content (TBS), and tibia ash content (TAC). Tibia diameters were measured at the narrowest and widest points, and then averaged. Assuming the tibia as a cylinder, TW, TL, and TDIAM measurements were used to derive the tibia variable tibia density (TDEN). Meat from both tibias was removed before conducting all the measurements.

TBS was measured with an Instron Materials Tester (model 5500, Instron Corp., Canton, MA) with Automated Materials Test System software version 4.2. The deformation rate was 5 mm/min. Tracing of force was recorded at a constant rate and the graphs showed plateau curves of maximal force (kilograms) reached to measure of the energy stored in the bone. Details of the TBS data collection has been described by Shim et al. (2012). TMC and TMD were measured by dual-energy X-ray absorptiometry. DXA scans were performed by using a Lunar Prodigy densitometer (GE Medical Systems, Waukesha, WI) operated in the small-animal mode. TMC and TMD measurements by DXA are defined as the amount of bone mineral in grams in the scan region, and the amount of TMC normalized to the scan region in centimeters squared, respectively (Cauley et al., 2005; Foutz et al., 2007).

After DXA assessment, left tibia was used for determination of percentage of ash on a fat-free dry weight basis, according to AOAC International (2005; method 992.16). Bird handling and study protocols were in line with the University of Georgia Animal Use and Care Guidelines.

Statistical Analysis

After editing 2,257 birds were recorded for BWG 0 to 4, BWG 0 to 6, and RFI 5 to 6. Number of birds with records for SW, SL, SDIAM, TW, TL, TDIAM, TDEN, TBS, TMD, TMC, and TAC ranged from 1,783 to 2,051. Descriptive statistics were obtained using PROC UNIVARIATE procedures of SAS version 9.1.3 (SAS Institute, 2006).

The genetic analysis was carried out using a Bayesian approach implemented via Gibbs sampling. After exploring the data with a multiple animal mixed model for the joint analysis of growth and bone quality traits, it was decided to implement single-trait analyses to obtain heritability estimates and 2-trait analyses,
considering all possible combinations of traits, to obtain genetic correlations. The linear mixed model used was:

\[ y_{ijnk} = H_i + S_j + u_n + e_{ijnk} \]  

(1)

where \( y_{ijnk} \) was the observed BWG 0 to 4, BWG 0 to 6, RFI 5 to 6, SW, SL, SDIAM, TL, TDIAM, TDEN, TBS, TMD, TMC, and TAC for bird \( n \), \( H_i \) (i = 1, 2, ... 8) was the fixed effect of the hatch class \( i \), \( S_j \) was the fixed effect of sex \( j \) (j = 1, 2) of bird \( n \), \( u_n \) was the random additive effect of bird \( n \), and \( e_{ijnk} \) was the random residual term. Assuming normality conditionally on the model parameters, the joint distribution of each pair of traits is expressed in matrix notation as:

\[ y|\beta, u, R_0 \sim N(X\beta + Zu, R_0 \otimes I) \]  

(2)

where \( y = (y_1', y_2')' \) is the vector of responses \( (y_i) \); \( \beta \) and \( u \) are vectors of systematic and random effects, respectively; and \( R_0 \) is a 2 \( \times \) 2 residual (co)variance matrix. \( X \) and \( Z \) are known incidence matrices. The Bayesian implementation, via Markov Chain Monte Carlo methods, of the model observed in Eq. (1) was carried out following Rekaya et al. (2013). The following priors were assumed to the unknowns in the model,

\[ p(\beta) \sim U[-10^6, 10^6] \]

\[ p(u|A, G) \sim N(0, G_0 \otimes A) \]

and for the elements of matrix \( G_0 \),

\[ p(g_{ii}) \sim U[0, 10^5] \text{ for } i = 1, 2, \]

and \( p(g_{ij}) \sim U[-\sqrt{\sigma_{g_{i}g_{j}}^2}, \sqrt{\sigma_{g_{i}g_{j}}^2}] \) for \( i \neq j = 1, 2, \)

where \( A \) is the additive genetic relationship between birds, \( G_0 \) is the additive genetic (co)variance matrix, and \( g_{ii} \) is the genetic variance for the trait \( i \). Similar priors are assumed for \( R_0 \) but with \( 10^6 \) for the upper bound of the uniform distribution for the diagonal elements. In the single-trait model, \( \text{var}(u) = A g_{ii} \) for \( i = 1, 2, \ldots 14 \), and \( \text{var}(y) = L\sigma_e^2 \), where \( \sigma_e^2 \) is the residual variance, and \( I \) is the identity matrix with the appropriate dimensions.

The resulting full conditional distributions needed for the implementation of Gibbs sampling for the systematic and random effects, and genetic and residual (co)variance matrices were in closed form being normal, and scaled-inverted Wishart, respectively. A unique chain of 200,000 samples was implemented where the first 50,000 samples were discarded as a burn-in period based on visual inspection of the behavior of the chain. Computer software developed by Rekaya et al. (2013) was used for analysis.

### Table 1. Descriptive statistics and heritability estimates of growth, feed efficiency, and bone quality traits in the Arkansas random-bred chicken population.

<table>
<thead>
<tr>
<th>Trait1</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWG 0 to 4 (kg)</td>
<td>2,257</td>
<td>0.82</td>
<td>0.12</td>
<td>0.26 (0.03)</td>
</tr>
<tr>
<td>BWG 0 to 6 (kg)</td>
<td>2,257</td>
<td>1.65</td>
<td>0.21</td>
<td>0.19 (0.04)</td>
</tr>
<tr>
<td>RFI 5 to 6 (g)</td>
<td>2,257</td>
<td>0.00</td>
<td>0.11</td>
<td>0.14 (0.03)</td>
</tr>
<tr>
<td>SW (g)</td>
<td>2,048</td>
<td>73.49</td>
<td>11.83</td>
<td>0.39 (0.07)</td>
</tr>
<tr>
<td>SL (mm)</td>
<td>2,049</td>
<td>76.70</td>
<td>5.79</td>
<td>0.35 (0.06)</td>
</tr>
<tr>
<td>SDIAM (mm)</td>
<td>2,051</td>
<td>10.57</td>
<td>1.81</td>
<td>0.09 (0.03)</td>
</tr>
<tr>
<td>TL (g)</td>
<td>1,840</td>
<td>13.14</td>
<td>2.69</td>
<td>0.34 (0.06)</td>
</tr>
<tr>
<td>TDIAM (mm)</td>
<td>1,950</td>
<td>100.26</td>
<td>5.39</td>
<td>0.54 (0.07)</td>
</tr>
<tr>
<td>TDEN (mg/mm²)</td>
<td>1,832</td>
<td>3.01</td>
<td>0.51</td>
<td>0.23 (0.05)</td>
</tr>
<tr>
<td>TBS (kg)</td>
<td>1,783</td>
<td>25.30</td>
<td>6.76</td>
<td>0.18 (0.04)</td>
</tr>
<tr>
<td>TMD (g/cm²)</td>
<td>1,947</td>
<td>0.12</td>
<td>0.02</td>
<td>0.13 (0.01)</td>
</tr>
<tr>
<td>TMC (g)</td>
<td>1,947</td>
<td>1.03</td>
<td>0.27</td>
<td>0.26 (0.04)</td>
</tr>
<tr>
<td>TAC (%)</td>
<td>1,965</td>
<td>40.13</td>
<td>3.04</td>
<td>0.08 (0.03)</td>
</tr>
</tbody>
</table>

1BWG 0 to 4 = body weight gain (0 to 4 wk); BWG 0 to 6 = body weight gain (0 to 6 wk); RFI 5 to 6 = residual feed intake (5 to 6 wk); SW = shank weight; SL = shank length; SDIAM = shank diameter; TL = tibia length; TDIAM = tibia diameter; TDEN = tibia density; TBS = tibia breaking strength; TMD = tibia mineral density; TMC = tibia mineral content; TAC = tibia ash content.

### RESULTS

Descriptive statistics and phenotypic correlations among traits are summarized in Tables 1 and 2, respectively. At the phenotypic level, BWG 0 to 4 and BWG 0 to 6 were positively correlated with both shank and tibia weights, lengths, and diameters ranging from 0.35 to 0.79. In contrast, TDEN showed negative associations with both growth traits (−0.24 and −0.31). While BWG 0 to 4 and BWG 0 to 6 had positive correlations with TBS, TMD, and TMC (0.08 to 0.72), they were negatively associated with TAC (−0.04 and −0.13, respectively); however, the relationship of BWG 0 to 6 with TAC was not significant (\( P > 0.05 \)). In general, the phenotypic association of RFI 5 to 6 with bone quality traits was weak (−0.02 to 0.08). Correlations among weight, length, and diameter of both shank and tibia bones were strong, ranging from 0.45 to 0.78, with the exception of those associations of SDIAM with TW and TL (0.16 and 0.28, respectively). While the association of TW with TDEN was weak and positive (0.15), the correlations of this latter trait with the rest of the bone morphological traits were negative, ranging from −0.07 to −0.58. Phenotypic associations of bone morphological traits with TBS and mineralization-related traits were positive, ranging from 0.24 to 0.75; however, those correlations with TAC were negative or close to zero, ranging between −0.12 and 0.06. TDEN showed negative correlations with TBS, TMC, TMD, and TAC (−0.08 to −0.35). Correlations among TBS and the mineralization-related traits were all positive (0.09 to 0.90). These relationships show that TBS was more strongly associated with TMD (0.70) than with TAC (0.23).

Heritability and genetic correlations of the traits are shown in Tables 1 and 2, respectively. Heritability of...
BWG 0 to 4, BWG 0 to 6, and RFI 5 to 6 was 0.26, 0.19, and 0.14, respectively. Heritability of morphological traits of bones ranged from 0.23 to 0.54 except for SDIAM which had a value of 0.09. TBS and the mineralization-related traits had heritability ranging from 0.08 to 0.26. Genetic relationship of growth with weight, length, and diameter of shank and tibia ranged from 0.37 to 0.80. In contrast, growth traits showed unfavorable genetic associations with TDEN, TBS, and TAC (−0.03 to −0.18). The mineralization-related traits TMD and TMC had positive genetic correlations with growth traits (0.06 to 0.65) but these latter ones showed an unfavorable association with TAC (−0.09 and −0.14).

In general, the genetic correlations of RFI 5 to 6 with the bone quality traits were positive or close to zero. Genetic associations among the weight, length, and diameter of shank and tibia were positive (0.34 to 0.99). In contrast, all these latter morphological traits (SW, SL, SDIAM, TW, TL, and TDIAM) had unfavorable genetic correlations with TDEN (−0.04 to −0.97). While TL showed unfavorable genetic associations with TBS and TAC (−0.23 and −0.88, respectively), TDIAM had an opposite genetic relationship with those tibia traits (TBS and TAC) (0.35 and 0.51, respectively). Shank and tibia weights, lengths, and diameters showed positive genetic correlations with TMD and TMC (0.09 to 0.85). Tibia density showed unfavorable genetic associations with TBS, TMD, TMC, and TAC (−0.13 to −0.51). Mineralization-related traits (TMD, TMC, and TAC) and TBS had positive genetic correlations (0.28 to 0.99).

**DISCUSSION**

The main objective was to study the genetic basis of bone quality traits and their relationship with growth in broiler chickens. However, important phenotypic trends were also identified. Growth was positively associated with size and weight of leg bones, tibia breaking strength, and with tibia mineralization level measured with DXA methodology (TMD and TMC). This should be expected, as bones are also components of the overall body weight of the bird (Sharman et al., 2007; Tszdzuiki et al., 2007; Zhou et al., 2007; Lewis et al., 2009; Barreiro et al., 2011). However, the size and weight of bones do not necessarily reflect quality. In the current study, bone quality was negatively correlated to growth. Fast growing birds had relatively less tibia mineralization compared to slow growing birds, when the bone ash was used as an indicator for bone mineral content, a phenomenon also observed by Rath et al. (2000). Frost and Roland (1991) and Seeman (1999) also showed the relationship between bone strength and bone mass. There are studies that suggest that growth rate is inversely related to bone mineralization, and that there is better mineralization (Corr et al., 2003; Brickett et al., 2007), density (Leterrier and Nys, 1992), and biomechanical properties (Pitsillides et al., 1999;

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Table 2. Genetic (above diagonal) and phenotypic (below diagonal) correlations of growth, feed efficiency, and bone quality traits in the Arkansas random-bred chicken population.

<table>
<thead>
<tr>
<th>Trait</th>
<th>BWG 0 to 4</th>
<th>BWG 0 to 6</th>
<th>BWG 5 to 6</th>
<th>RFI 5 to 6</th>
<th>SDIAM</th>
<th>TW</th>
<th>TDAM</th>
<th>TBS</th>
<th>TMD</th>
<th>TMC</th>
<th>TAC</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWG 0 to 4</td>
<td><strong>0.82</strong></td>
<td><strong>0.77</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.76</strong></td>
<td>-0.01</td>
<td>0.73</td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>BWG 0 to 6</td>
<td>-0.01</td>
<td><strong>0.82</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.81</strong></td>
<td><strong>0.73</strong></td>
<td>-0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>BWG 5 to 6</td>
<td>-0.01</td>
<td>-0.01</td>
<td><strong>0.82</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.76</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>RFI 5 to 6</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td><strong>0.82</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.76</strong></td>
<td>0.01</td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>SDIAM</td>
<td><strong>0.73</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.76</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>TW</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
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<tr>
<td>TDAM</td>
<td><strong>0.73</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.76</strong></td>
<td><strong>0.81</strong></td>
<td>-0.01</td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
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<tr>
<td>TBS</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td>0.01</td>
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<tr>
<td>TMD</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
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<tr>
<td>TMC</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
</tr>
<tr>
<td>TAC</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td><strong>0.73</strong></td>
<td><strong>0.81</strong></td>
<td>0.01</td>
<td><strong>0.73</strong></td>
</tr>
</tbody>
</table>

*P* values: **0.001, *P* < 0.001, *P* < 0.01.
Tibia breaking strength was positively associated with bone traits in the current study except density. Bone strength is not determined by a single factor but by a series of bone characteristics (Turner, 2002; Currey, 2003; Davidson et al., 2006; Seeman and Delmas, 2006) including mass, ash content, mineral density, (Rath et al., 2000), size, shape, (Rath et al., 1999; Turner, 2006), and loading-induced modifications (Foutz et al., 2007; Rawlinson et al., 2009). Corr et al. (2003) reported that heavier birds had broader bones, but these bones had smaller mineral content compared to lighter chickens. This could also explain the negative association between growth and TAC and TDEN. Therefore, the bone mineralization indicators (TMD, TMC, and TAC) could be considered as important parameters in assessing biomechanical integrity of bones. Among the 3 parameters, TMD is the easiest to measure and also has the strongest phenotypic correlation with TBS.

Heritability of weight and length of both leg bones were within the range of values (0.16 to 0.62) estimated from chicken (Merritt, 1966; de Verdal et al., 2013) and turkey populations (Abplanalp and Kosin, 1952; Kondra and Shoffner, 1955; Johnson and Asmundson, 1957; McCartney, 1961; Krueger et al., 1972; Havenstein et al., 1988). In contrast, heritability of shank and tibia diameters were lower than reported estimates of 0.33 to 0.46 for shank diameter and 0.74 for tibia diameter in turkeys (Nestor et al., 1985; Havenstein et al., 1988) and broiler chickens (de Verdal et al., 2013). Heritability of tibia density was lower than the 0.62 to 0.65 reported by Havenstein et al. (1988) for turkeys; however, it should be pointed out that they used a different method to assess these traits. Likewise, heritability of tibia breaking strength was lower than the 0.30 to 0.80 reported for broiler chickens (Mandour et al., 1989; de Verdal et al., 2013) and White Leghorn hens (Bishop et al., 2000). We are not aware of heritability estimates on TMD and TMC in broiler chickens. In mice and humans, heritability for of bone mineral density, corresponding to either the whole body or several different types of bones, ranged from 0.35 to 0.84 (Ng et al., 2006; Klein et al., 1998; Park et al., 2012; Wagner et al., 2013). Heritability for TAC was lower than the reported estimate of 0.41 (de Verdal et al., 2013).

Given the low heritability of SDIAM and TAC, other nongenetic strategies may be beneficial than genetic improvement. Heritability of the growth traits, ranging from 0.19 to 0.26, and that of RFI was 0.14, were lower than the estimates reported by Rekaya et al. (2013) for commercial broiler population for the period 6 to 7 weeks of age. Estimated genetic correlations between length and weight of each leg bone (shank and tibia) were between 0.72 and 0.84 in turkeys (Havenstein et al., 1988). Therefore, weight and length of the bone could be influenced by common additive genetic factors.

Current genetic correlations of growth with shank length and tibia were within the range reported for chickens (Merritt, 1966; de Verdal et al., 2013) and for turkeys (Johnson and Asmundson, 1957; McCartney, 1961; Krueger et al., 1972; Havenstein et al., 1988). The genetic association of growth with tibia length and tibia diameter found in the current study differs from the study by de Verdal et al. (2013), who reported negative genetic correlations of body weight of broiler chickens at 23 days of age with tibia length (−1.00) and tibia diameter (−0.95). Overall, our observations indicated that genetic factors influencing faster growth also lead to heavier, longer, and wider leg bones. The current study shows that the genetic association between TMD and TMC is positive, but not as strong as the observed phenotypic correlation (0.90). Tibia mineral content had a stronger association with the direct assessment of the mineralization level of the bone (TAC), than that of TMD with TAC. Thus TMC would be a more suitable noninvasive method for improvement of bone quality. There genetic correlation between growth and tibia ash (i.e., TAC) was negative (−0.22) similar to that reported by de Verdal et al. (2013). Although the other mineralization-related traits (TMD and TMC) showed a positive genetic association with growth traits, the relationship between TAC and growth should be more relevant, given the strength of the genetic association of TAC with TBS (0.99) and the importance of TBS as an indicator trait of skeletal integrity (Turner, 2006; Rath et al., 2000). It appears that selection for growth may have impacted legs (Lilburn, 1994; Webster, 1995), which may be due in part to asynchrony between body mass and bone development (Rath et al., 2000; Dibner et al., 2007; Shaw et al., 2010). Thus, fast growth could have some negative effects on leg bone mineralization.

Unlike previous studies with commercial broiler chickens (de Verdal et al., 2013) and laying hens (Bishop et al., 2000) that reported a favorable genetic association between growth and TBS (0.93 and 0.33, respectively), the current results suggested a negative relationship between growth and TBS. Likewise, we observed that TBS would not be favored when selecting for better feed efficiency. A similar observation was also made by de Verdal et al. (2013). Genetic correlations of TBS with TL and TW were −0.70, and 0.69, respectively, which was similar to previous commercial broiler study (de Verdal et al., 2013). Therefore, genetic factors favoring TW would have similar or favorable effects on TBS. The importance of bone weight and TBS relies on the mineral phase which constitutes about 70% of the bone mass. The mineral content of the bone is a
main determinant of its biomechanical properties (Rath et al., 2000; Currey, 2003). In contrast, promoting larger tibias by selection would have detrimental effects on TBS.

**CONCLUSIONS**

Bone quality traits showed additive genetic variation, implying that they can be improved through selection. It appears that genetic selection for growth is negatively correlated with some traits involved in the integrity, health, and maturity of leg bones. The improvement of the mineralization level of the bone would enhance its quality and strength which would be reflected in an improved welfare.

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