Genetics of Phytate Phosphorus Bioavailability: Heritability and Genetic Correlations with Growth and Feed Utilization Traits in a Randombred Chicken Population[1]

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ABSTRACT The current study was undertaken to estimate variance components for phytate P bioavailability (PBA) and the genetic correlations among PBA with growth and feed utilization (or intake) traits in an unselected random mating chicken population. Pedigreed data from 901 Athens-Canadian randombred chickens hatched from 26 sires, 71 dams, and 105 grandparents were used for estimation of genetic parameters. Birds were individually housed in metabolic cages at 4 wk of age and fed a 0.35% P diet. After 3 d of acclimatization, excreta produced for 3 consecutive d were collected and feed consumed (FC) was measured. Individual 4-wk BW and BW gain (BWG) during the 3-d excreta collection period were also measured. Feed conversion ratios (FCR) were calculated. Phytate P bioavailability was estimated from the disappearance of phytate during the passage of feed through the gastrointestinal tract. The restricted maximum likelihood method with the average information matrix algorithm was used for the estimation of variance components. The heritability estimate for PBA was about 0.10. Genetic correlations between PBA and BW, BWG, and FC were moderate and negative, indicating that improving PBA utilization would moderately affect growth. The genetic correlation between PBA and FCR was negligible and suggested that selection for PBA will not adversely affect FCR. The economic implications of genetically modifying poultry to improving phytate P utilization and the subsequent elimination or reduction of the amount of phytase used in poultry diets are yet to be determined.

(*Key words*: average information matrix, bioavailability, heritability, phosphorous, phytate)

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INTRODUCTION

Phosphorus is an essential mineral required in poultry diets for normal growth and development. It plays an important role in the metabolism of carbohydrates, amino acids, and lipids. To meet metabolic demands, birds of each species and age require specific amounts of P readily available for absorption and utilization. Poultry diets are made primarily of ingredients of plant origin, including cereal grains, cereal by-products, and oil seed meals. Phytate P constitutes a major portion (approximately 60 to 80%) of the total P in seeds of cereals, grain, legumes, and oil-bearing plants (Ravindran et al., 1994). Poultry have a very limited ability to utilize phytate P due to the lack of adequate levels of endogenous phytase (Heuser et al., 1943). This inadequacy results in a substantial loss of P through excreta and creates a significant pollution threat when manure containing residual P is applied to land (Ravindran et al., 1995). Several studies have shown that supplementing poultry diet with exogenous phytase can improve the availability of phytate P in chickens (Simons et al., 1990; Perney et al., 1993; Ravindran et al., 1995).

An alternative solution to improving the low utilization efficiency of phytate P in poultry is by genetic manipulation. While no studies on genetic improvement of phytate P utilization in poultry have been reported, several researchers (Nelson, 1976; Edwards, 1983; Ravindran et al., 1995; Zhang et al., 1998) have suggested that there is genetic variance for the ability to utilize phytate P in chickens. However, phytate P utilization has been shown to depend on strain, age, ingredient type, and dietary levels of Ca (Edwards, 1983), inorganic P (Ravindran et al., 1995), and vitamin D (Edwards, 1993). Punna and Roland (1996) demonstrated that the variation in phytate P utilization in chickens was related with growth, livability, and skeletal strength among individual broilers of the same strain. Carlos and Edwards (1997) observed large individual differ-

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Abbreviation Key: ACRB = Athens-Canadian randombred; BWG = body weight gain; FC = feed consumed; FCR = feed conversion ratio; PBA = phytate phosphorus bioavailability; REML = restricted maximum likelihood; TRE = total random effect.

ences in phytate P utilization within a strain when fed P deficient diets with or without phytase. Zhang et al. (1998) reported that chickens from an unselected control line utilized phytate P better and had improved livability, mortality, and growth when compared with their counterparts selected for either increased or decreased incidence of tibial dyschondroplasia. Smith et al. (2001) demonstrated a relationship between phytate P utilization and progeny BW and bone mineralization. The objective of the present research was to establish a pedigreed base population from an unselected random-mating chicken population for the estimation of heritability of phytate P bioavailability (PBA) and genetic correlations of PBA with growth and feed utilization (or intake) traits.

MATERIALS AND METHODS

Birds

Data were collected from an unselected random mating Athens-Canadian randombred (ACRB) chicken population (Hess, 1962). Twenty-six males were pedigree mated to 71 dams (sex ratio 1:2~3) to hatch 1,004 chicks in six hatches at 7-d intervals. Chicks were placed in pens with litter and fed a corn and soybean meal based diet containing 23% protein, 3.2 kcal ME/kg, 0.90% Ca, 0.675% total P, and 0.45% available P until 4 wk of age. At 4 wk of age, birds were transferred to individual metabolic cages and fed the same diet with the mineral source of P largely removed and Ca and total P adjusted to 1.06 and 0.35%, respectively. After 3 d of acclimatization, excreta produced during 3 consecutive d were collected and feed consumed (FC) was measured. Individual 4-wk BW and BW gain (BWG) during the 3-d excreta collection were also measured. Excreta were oven-dried at 80°C and ground. Phytate P in the feed and dried excreta was determined by method described by Latta and Eskim (1980). Disappearance of phytate during passage of feed through the gastrointestinal tract was considered as the indicator of phytate P utilization (Ravindran et al., 1995). The PBA was estimated as follows:

$$\text{PBA} = (\text{A} - \text{B})/\text{A} \times 100\%$$

where A = phytate P content in feed (%) × feed intake (g), and B = phytate P content in dried excreta (%) × dried excreta weight (g).

Body weight, BWG, FC, feed conversion ratio (FCR) for BW, and PBA data were collected on 1,004 birds. The FCR was calculated as the ratio of FC per BWG during the excreta collection period.

Data Editing and Statistical Analysis

The PROC ANOVA (SAS Institute, 1998) was used to obtain descriptive statistics of the traits, testing the significance of sex and hatch group effects, estimating the total random effect for PBA, and assessing normality and homogeneity. The saturated model was

$$Y_{ijk} = \mu + S_i + H_j + SH_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} = individual observation for a trait, μ = overall mean, S_i = sex effect (i = 1,2), H_j = hatch group effect (j = 1,2…6), SH_{ij} = interaction effect of sex and hatch group, and ε_{ijk} = individual total random effect. Individuals with trait data beyond three standard deviations from the estimated sample mean were considered as outliers and consequently were removed from the data set. After data editing, 901 individuals with complete data sets from 26 sires, 71 dams, and 105 (44 males and 61 females) grandparents were used for estimation of genetic parameters. The individual quantity of the total random effect (TRE), which was the sum of additive genetic effects and residuals, was calculated by subtracting the least square estimates for the fixed effects from the observed values.

Mixed animal models (Mrode, 1996) and restricted maximum likelihood (REML) (Henderson, 1985) methods were used for estimating the variance components of the traits measured. The animal model used was

$$\text{y} = \text{X}\beta + \text{Zu} + \text{e}$$

where, $\text{y} = (\text{y}_1', \text{y}_2' \ldots \text{y}_t')'$ and y_t' is the vector of phenotypic observations for trait t; X = matrix that relates fixed effects to the phenotypic record; Z = matrix that relates animals to the records; $\beta = (\beta_1', \beta_2' \ldots \beta_t')'$, and β_t' = vector of fixed effects for trait t'; $\text{u} = (\text{u}_1', \text{u}_2' \ldots \text{u}_t')'$, and u_t' = vector of random animal effects for trait t; $\text{e} = (\text{e}_1', \text{e}_2' \ldots \text{e}_t')'$, and e_t' = vector of residual effects for trait t. The variances of random animal effects were var(u) = A ⊗ G and var(e) = I ⊗ R, where A = additive relationship matrix, G = (co)variance matrix for genetic effects of the traits, I = identity matrix, R = (co)variance matrix for the corresponding residual effects. For a univariate model, $\text{G} = \sigma_a$ and $\text{R} = \sigma_e$.

Sex and hatch groups were considered as fixed effects. Heritability estimates and genetic and phenotypic correlations were estimated for PBA, BW, BWG, FC, and FCR. A univariate model was used to estimate heritability for each trait and a multvariate model was used to estimate the genetic and phenotypic correlations. Pedigree information of the parents was utilized, and the formation of the inverse of the A-matrix (A^{-1}) was based on methods of Henderson (1975) and Quaas (1976). The estimations of variance components were accomplished with the average information algorithm for REML (Johnson and Thompson, 1995). Convergence was considered to have been reached when

$$(\hat{\theta}_t - \hat{\theta}_{t-1})'(\hat{\theta}_t - \hat{\theta})/\hat{\theta}_t'\hat{\theta}_t < 5 \times 10^{-11}$$

where $\hat{\theta}_t$ is the vector of estimated parameters in t iteration. The estimates of genetic parameters were calculated according to the definitions (Falconer and Mackay, 1996) and obtained from the estimated (co)variance matrices for genetic and residual effects. The standard errors of heritability were based on the asymptotic variances of $f(\hat{\theta}_t)$ (Stuard and Ord, 1994; Dodenhoff et al., 1998) and calculated as

TABLE 1. Means, SD, CV, and range of phytate P bioavailability (PBA), BW (4 wk), BW gain (BWG), feed consumption (FC), and feed conversion ratio (FCR) during a 3-d period in a random mating control population of chickens (n = 901)

Trait	Mean ± SD	CV (%)	Minimum	Maximum
PBA (%)	30.88 ± 7.37	23.87	12.84	48.98
BW (g)	289.62 ± 42.28	14.60	181.20	399.10
BWG (g)	43.83 ± 10.02	22.86	21.00	73.60
FC (g)	101.02 ± 16.53	16.36	56.60	146.10
FCR (g:g)	2.36 ± 0.37	15.68	1.33	3.36

$$SE(h^2) \approx \sqrt{\left\{\frac{\partial h^2}{\partial \theta'}\right\} \text{var}(\hat{\theta}) \left\{\frac{\partial h^2}{\partial \theta}\right\}} \quad \frac{\partial h^2}{\partial \theta'} = \left[\frac{h^2 - h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2}\right]$$

where var($\hat{\theta}$) was composed of the elements of an asymptotic dispersion matrix of the estimated parameters [(co)variance components], which is the inverse of the negative average information matrix. For $SE(h^2)$, $\theta = [\sigma_a^2, \sigma_e^2]$.

RESULTS AND DISCUSSION

Means, SD, CV, and minimum and maximum values for the traits measured are listed in Table 1. The range of PBA is consistent with the observations of Edwards (1983). The variability in PBA was about 24%. The ANOVA results (data not shown) of the fixed model showed that there were differences ($P \leq 0.05$) among hatch groups for all the traits. As much as there were differences among hatch groups, the within hatch group variability was constant, indicating homogenous variances among hatch groups. The trait data were corrected for hatch group effects, and the least square means for the traits for both sexes are presented in Table 2. There were sex differences ($P \leq 0.05$) for BW, BWG, FC, and FCR; however, PBA exhibited no sexual dimorphism ($P > 0.05$).

The distribution profile of PBA is shown in Figure 1. The normal Q-Q plot (Figure 2) of TRE shows that the distribution had no apparent departure from normality. Figures 1 and 2 strongly suggest that PBA follows the classical characteristics of a quantitative trait. The experimental birds were sampled from an unselected random mating population; therefore the distribution of TRE reflected the sampling properties of PBA. Normality of PBA and homogeneity of variances within hatch groups indicated that the assumptions y ~ N(Xβ, V) for REML methodology were met in variance component estimation for PBA.

The estimates of variance components and heritability for measured traits are shown in Table 2. The heritability of PBA from the univariate and multivariate models was about 0.10, and the standard error for the estimate was small. This result demonstrates that there was some additive genetic variation associated with PBA in this line; however, genetic improvement by mass selection would be difficult. Many researchers have shown that the utilization of phytate P is strongly associated with the dietary level of Ca, inorganic P, and vitamin D_3 (Scheideler and Sell, 1987; Mohammed et al., 1991; Edwards, 1993; Ravindran et al., 1995). This suggests that phytate P utilization is conditioned upon dietary components and the estimated genetic parameter is only valid under the nutritional environment used in the current experiment. In the present study, a diet was used with a suboptimal level of total P, a dietary condition under which phytate P is suggested to have a higher availability in chickens (Edwards, 1993). Under commercial dietary conditions phytate P availability might be different and a new genetic parameter estimation may be required. Analysis of variance with TRE showed that there were no sex differences for PBA, and consequently heritability (0.09 ± 0.03) was estimated after dropping the sex effect. Equality of the heritability estimate with or without sex as a fixed effect indicates that PBA at 4 wk is not affected by sex.

The heritablity estimates for BW, BWG, and FC were consistent with values reported in the literature (Chambers, 1990). The heritability estimate for FCR was lower than the modest estimates (0.2 to 0.4) reported by Pym (1990) and Chambers et al. (1994). Feed consumption data were obtained during the 3-d excreta sampling period at 4 wk

TABLE 2. Least square means (LSMEAN), variance components and estimates of heritability (h^2) for phytate P bioavailability (PBA), BW (4 wk), BW gain (BWG), feed consumption (FC), and feed conversion ratio (FCR) during a 3-d period in a random mating control population of chickens

	LSMEAN ± SE		Variance components[1]		
Trait	Male (n = 435)	Female (n = 466)	σ_A^2 ± SE	σ_e^2 ± SE	h^2 ± SE
PBA (%)	31.22 ± 0.31[a]	31.48 ± 0.32[a]	3.71 ± 1.31	36.41 ± 1.57	0.09 ± 0.03
BW (g)	306.79 ± 1.82[a]	273.23 ± 1.88[b]	919.64 ± 155.82	617.57 ± 89.43	0.60 ± 0.07
BWG (g)	47.02 ± 0.42[a]	41.51 ± 0.43[b]	15.72 ± 3.62	60.59 ± 3.14	0.21 ± 0.04
FC (g)	107.41 ± 0.62[a]	95.89 ± 0.64[b]	64.20 ± 12.14	05.80 ± 8.08	0.38 ± 0.06
FCR (g:g)	2.34 ± 0.02[a]	2.37 ± 0.02[b]	0.08 ± 0.03	0.12 ± 0.05	0.07 ± 0.03

[a,b]Traits for males and females with no common superscript are significantly different ($P \leq 0.05$).

[1]σ_A^2 = additive genetic variance; σ_e^2 = residual variance.

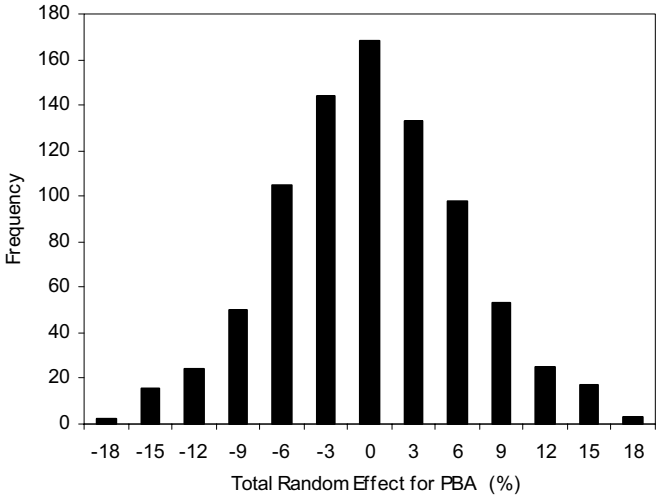

FIGURE 1. The distribution for the total random effect (additive genetic effect + residual) of phytate P bioavailability (PBA) in a control population of chickens.

of age. The short duration of the test period might have contributed to the poor heritability estimate for FCR. In addition, at this age, the maintenance requirement may substantially mask genetic variation of feed efficiency for growth (McCarthy and Siegel, 1983; Marks, 1991).

Phenotypic and genetic correlations among the traits were obtained with a multivariate REML method, and the results are presented in Table 3. The phenotypic correlations between PBA and BW, BWG, FC, and FCR were low. Phenotypic correlations among growth- and feed-related traits were consistent with other reports (Chambers, 1990). The low phenotypic correlations may be a reflection of the stability of the environment in which the birds were raised. Genetic correlations between PBA and BW, BWG, and FC were moderate and negative, which indicated that improving PBA utilization would moderately affect growth. The negative genetic correlation between PBA and FC may be due to the fact that secretion of endogenous phytase cannot keep up with FC. The modern commercial broiler has been selected for fast growth, and the moderately antagonistic relationship between growth and PBA might have contributed to the inability of commercial broilers to utilize phytate P. The negative genetic relationship between PBA and growth rate was demonstrated by Edwards (1983), who showed that ACRB birds utilized phytate P better than modern commercial birds. The negative relationship between PBA and growth may be related to the rate of feed passage. Modern broilers consume more feed and have a higher rate of passage than ACRB birds, which would run contrary to good phytate P utilization. Incorporating PBA into a selection index for genetic improvement would moderately curtail growth improvement. At present, the enzyme phytase is added to poultry diets to enhance phytate P utilization at the current growth levels. The economic implications of genetically modifying poultry to improving phytate P utilization and the subsequent elimination or reduction of the amount of phytase used in poultry diets are yet to be determined.

The genetic correlation between PBA and FCR was low, indicating that selection for PBA would not adversely affect FCR, at least for the ACRB population. The genetic relationship between growth- and feed-related traits has been discussed extensively in literature (see Chambers, 1990). The current study is the first to report on the genetics of PBA and its relationship with growth. A comprehensive relationship among PBA, growth, and feed-related traits and reproductive capacity is needed before any breeding strat-

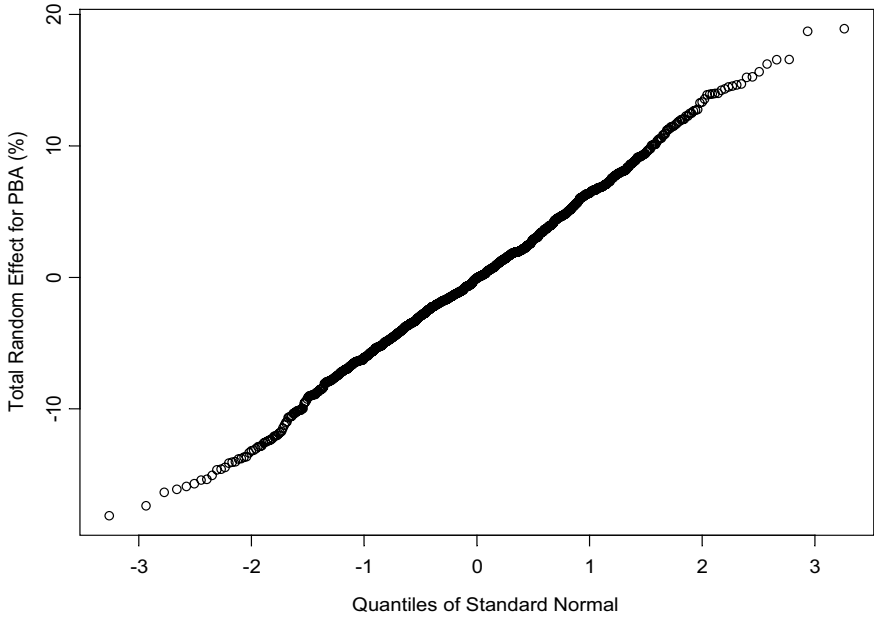

FIGURE 2. The normal Q-Q plot for the total random effect (additive genetic effect + residual) of phytate P bioavailability (PBA) in a control population of chickens.

TABLE 3. Genetic (above diagonal) and phenotypic (below diagonal) correlations among phytate P bioavailability (PBA), BW (4 wk), BW gain (BWG), feed consumption (FC), and feed conversion ratio (FCR) in a random mating control population of chickens

Trait	PBA	BW	BWG	FC	FCR
PBA		–0.52	–0.38	–0.44	–0.03
BW	–0.07		0.78	0.78	–0.18
BWG	0.16	0.38		0.93	–0.13
FC	0.11	0.67	0.70		
FCR	–0.11	0.13	–0.69	–0.00	

egy is devised. It would also be worthwhile to examine the genetic variability in commercial breeder lines fed commercial diets and also collect data beyond 3 d.

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