SELECTION FOR PHYTATE PHOSPHORUS BIOAVAILABILITY IN POULTRY

by

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(Under the direction of Samuel E. Aggrey)

ABSTRACT

A divergent selection experiment for phytate phosphorus bioavailability (PBA) was undertaken for 3 generations using the Athens-Canadian Randombred (ACRB) chickens. Thirty-five sires and 105 dams were used to generate the base population (G_0). 951 individuals in G_0 were measured and were ranked according to their hatch-corrected PBA values to establish the divergent sub-populations. For each line, 12 males and 36 females from individuals with highest or lowest hatch-corrected phenotypic values (or breeding values in high PBA line at G_2) were selected as breeders. At generations 1-3 (G_1-G_3), about 430 individuals per line were measured. PBA was estimated from the disappearance of phytate during the passage of feed through the gastrointestinal tract under a diet containing a suboptimal level of phosphorus in ration. The heritability of PBA and the genetic correlations with body weight (BW), BW gain (BWG), feed intake (FC) and feed conversion ratio (FCR) were estimated with the restricted maximum likelihood (REML) procedure and an animal model. The direct and correlated responses were investigated with fixed effect models and mixed model methodology. Following main results and conclusions were obtained.

(1) The inheritance of PBA was not apparently deviated from an additive model of many loci and the heritability was low (0.07 ± 0.02 - 0.09 ± 0.03). The estimates using a pooled data set combining G_0 and either high or low PBA line were the same as or close to that with the data

of G_0 exclusively. The combination of the data sets of the divergent lines led to a lower estimate (0.05 ± 0.02). (2) Selection for PBA proved to be feasible. At G_3, the cumulated divergent response (Rc) reached 2.56% ($P<0.01$). The realized heritability (0.03-0.06) was lower than the estimated values. Best linear unbiased prediction (BLUP) selection was more efficient than individual phenotypic selection. (3) The means of phenotypic values of PBA fluctuated across generations. This implies that, from the short-term selection experiment, it is difficult to establish any trend on the phenotypic level. (4) The least square analysis based on line comparisons detected the divergent selection response but did not indicate the true genetic changes that occurred in each line. The application of mixed model methodology proved to be valid in the separation of observed change into its environmental and genetic components. (5) With the data of the base population (G_0) exclusively, the estimated genetic correlations of PBA with BW, BWG and FC were negative and moderate. This was verified by the cumulated divergent correlated responses (DCR_C) in these traits. However, the correlated responses were asymmetric, and were mainly attributed to the genetic changes that occurred in the upward selection line. (6) The negative genetic correlations of PBA with BW, BWG and FC became much weaker or even reversed in direction when the information from the selected generations (G_1 - G_3) were combined with the data of G_0 to estimate (co)variance components. There was line dimorphism in the changes.

INDEX WORDS: Bioavailability, BLUP, Genetic parameter, Genetic trend, Phytate, Phosphorus, Poultry, REML, Selection, Variance components

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DEDICATION

I wish to dedicate this thesis to my grandmother and parents for their unending love and education throughout my life. I am thankful to my wife, Li Zhu for her support and encouragement in my study.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Phosphorus (P) is an essential mineral required in poultry diets for normal growth and development. It is a major constituent of bone and plays an important role in the metabolism of carbohydrates, amino acids and lipids. To meet metabolic demands, poultry of each species and age require specific amounts of phosphorus readily available for absorption and utilization. In the diets of broiler chickens, the recommendation of available phosphorus varies from 0.45 % to 0.3%, depending on the age of the broiler (NRC, 1994). In laying hens, 0.21 - 0.35 % available phosphorus in the diet is required to meet metabolic requirements. Poultry diets are made primarily of ingredients of plant origin, including cereal grains, cereal by-products and oil seed meals. About 70% of all phosphorus in plant products (cereals, grain legumes, and oil bearing plants) is present as phytate (phytic acid and its salts) (Ravindran et al, 1994). Poultry have very limited ability in utilizing 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 resource and creates a significant pollution threat when manure containing residual P is applied to land (Ravindran et al, 1995). Many studies showed supplements of external phytases and vitamin D_3 can improve the availability of phytate P in chickens (Edwards, 1993; Ravindran et al, 1995; Simons et al, 1990;). Another possible approach to improve the low utilization efficiency of phytate P in poultry is a genetic manipulation. While no effort for the genetic improvement of the efficiency in poultry industry has been reported yet, several researchers have suggested that there is genetic variance for the ability to utilize phytate P in chickens. Edwards (1983) found the average retention percentage of phytate P differed among strains when the diet had suboptimal levels of P and the difference was accentuated by high levels of calcium in the ration. Punna and Roland (1996) demonstrated that the variation in phytate P utilization in the same strain of chickens was related with growth, livability and skeletal strength among individual broilers of the same strain.

Carlos and Edwards (1997) observed large individual differences in phytate P utilization within a strain when fed a P deficient diet with or without phytase. The differences between strains and the large variability within a strain suggest that the trait can be improved by selection. Genetic approach can provide us with a permanent, long-term solution to the low efficiency of poultry in utilizing phytate P and the resulted environmental pollution.

The main goal of this research is to ascertain the efficacy of improving phytate P bioavailability (PBA) in birds through genetic manipulation.

OBJECTIVE

(1) Establish a foundation chicken population for the estimation of genetic parameters:

(a) Estimate heritability of PBA;

(b) Estimate genetic correlation of PBA with growth and feed utilization traits.

(2) Short - term selection for PBA (3 generations):

(a) Evaluate the direct response to selection.

(b) Evaluate the correlated responses of growth and feed utilization traits to selection for PBA.

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CHAPTER 2

LITERATURE REVIEW

2.1 The Utilization of Phytate Phosphorus in Poultry

The utilization efficiency of phytate phosphorus (P), which constitutes the major proportion of plant P, has been studied extensively by nutritionists for about 40 years. The most common response criteria for the utilization of phytate P are weight gain and percent bone ash. Shell quality and bone health scores are also used frequently in layers and broilers, respectively. Radioactive labeled phytate P (P^{32}) was used to study retention in earlier studies (Nelson, 1967).

A quantitative criterion, which has been employed in most studies, is phytate P bioavailability or retention. It is usually defined as the percentage of the phytate that is hydrolyzed during the passage of feed through the total track of animals (Ravindran et al., 1995). Literature on phytate P utilizing ability in birds has been conflicting. In earlier literature, most investigators observed that natural phytate was a poor P source for various species of poultry. Heuser et al. (1943) presented evidence indicating the P from cereals and legumes at levels of 0.38 and 0.65% did not promote normal bone development in chicks in spite of the presence of adequate vitamin D. Gillis et al. (1948) reported that chicks receiving 0.2% inorganic and 0.4% phytin P showed apparent depression of growth and bone development, while 0.2% phytin P and 0.4% inorganic P resulted in normal growth and bone development. Gillis (1957) fed chicks and turkeys P^{32} labeled calcium phytate and P^{32} labeled monosodium *ortho* phosphate and then measured the amount of radioactivity retaining in tibia. They concluded that chicks utilized the P in calcium phytate only 10% effectively as that in sodium salt and the relative utilization of phytate P by the turkey was less than 2%.

On the other hand, effective utilization of phytate P was also reported in a few studies where diets contained substantial percentages of ingredients that were rich in plant phytases (Sieburth et al., 1952; Singsen, 1947; Temperton et al. (1965a, b). Singsen (1947) found that

phytin P was satisfactory to meet the growth requirements of chicks but did not promote adequate bone calcification. Sieburth et al. (1952) reported that the P in finely ground flour of whole-wheat almost had the same nutritional value to chicks as inorganic P. Temperton et al. (1965a, b) also observed similar results in chicks, pullets and turkeys. Recent reports showed that poultry can utilize phytate P but the efficiency is low (Ballam et al., 1987; Edwards, 1983; Scheideler and Sell, 1987).

Phytate P bioavailability in poultry ranges from 0 to over 50% (Ravindran et al, 1995). Nelson (1976) observed that, when diet contains corn as the only grain, broilers 4 and 9 week in age and laying hens had 0, 2 and 8% phytate P hydrolyzed in the tracks, respectively, and when wheat replaced one half of corn, the corresponding values were 8, 13, and 13%, respectively. Temperton and Cassidy (1956a,b) reported that, when diets contained wheat as the main grain ingredient, up to 60% phytate P was hydrolyzed in the track of chicks and pullets, but feed intake, body weight at 8 weeks of age and tibial bone ash were improved in chicks receiving supplementary inorganic P. Edwards (1983) also reported high phytate P retention and the values ranged from 23-56% depending to strains of birds and the Ca level in the diets.

Ballam et al. (1984) demonstrated that phytate P hydrolysis ranged from 3 to 42%, depending on the levels of dietary calcium (Ca) and the source of fiber. Scheideler and Sell (1987) found that the retention of phytate P was up to 40% in hens 34 weeks of age and much lower in hens 56 and 73 weeks of age. Mohammed et al. (1991) reported 50.5% and 75.5% of phytate P digestibility when broilers were fed normal diet or low Ca and P diet. Similar results were reported by Edwards and his colleagues (Edwards, 1993; Mitchell and Edwards, 1996a, b).

2.2 Nutritional and Environmental Significances of the Utilization of Phytate P

2.2.1 The Effect of Phytate on Mineral Nutrition

In 100g dried material (DM) of several main feed ingredients, the contents of phytate P are: corn 0.17-0.29g, barley 0.19-0.33g, wheat 0.17-0.38g, sorghum 0.21-0.28g, soybean 0.37-0.42g, cottonseed 0.79-0.42g, peanut 0.48g, rapeseed 0.54-0.78g, and sunflower 0.89g, respectively (Ravindran et al., 1995). This means the content of phytate P in typical diets of layers or broilers will be over 0.2%. Phytate acid is a poly-anionic molecule with six phosphate groups and forms insoluble salts with divalent cations (Ca, Mg, Mn, Fe and Zn) in weak acidic to neutral pH conditions and, consequently, reduces their availability to rats (Brink et al., 1991; Davies and Nightingale, 1975; Davies and Olpin, 1979), pigs (Pallauf et al., 1994) and poultry (Edwards, 1966; Krarzer et al., 1959; Lease, 1966; O'Dell et al., 1964). When diets contain ingredients high in phytate, more Ca and other mineral nutrients would be required to offset the portion that was unavailable due to binding with phytate.

Nelson et al. (1968) found that Ca requirement of White Leghorn chicks fed a purified diet containing no phytate was 0.5%, and the requirement increased to 0.95% on a diet containing 1.25% phytic acid. Similarly, Farkvam et al. (1989) demonstrated that the calcium requirement for producing a given level of bone ash in growing broilers was increased with natural phytate in diets. Two studies reported that the reduction of Zn availability due to phytate decreased the growth rate, making Zn a limiting mineral in high-phytate diets (Davies and Nightindale, 1975; O'Dell and Savage, 1960). Conversely, the dephytinization of soybean improved Zn availability (Lonnerdal et al., 1989).

Furthermore, indirect evidence for the adverse influence of phytate on mineral nutrition and the beneficial effect of exogenous phytase has been provided. Many studies showed the

supplement improved the absorption and deposition of Zn, Mn, Mg, Cu and other trace mineral elements in chickens (Kim et al., 2002; Lim, et al., 2001; Mohanna and Nys, 1998; Qian, et al., 1996).

2.2.2 Effect of Phytate on the Utilization of Proteins and Energy

The nutritional significance of phytate is further complicated by protein-mineral-phytate interactions (Caldwell, 1992; Honing and Wolf, 1991). In the condition of low pH, phytic acid directly forms electrostatic linkages with several amino acids. As pH approaches the isoelectric point, complexes form through a bridge of Ca, Mg, Zn, and other divalent cations (Anderson, 1985, Ravindran, et al., 1995). The reduced solubility of proteins as a result of such complexes can adversely affect certain functional properties of proteins that are dependent on their hydration and solubility. Atwal et al. (1980) found improvements in protein utilization with decreasing levels of phytate in rat. Sattlerlee and Abdul-Kadir (1983) reported the effect of phytate on protein utilization was influenced by the protein source. Indirect evidences for phytate-proteins interaction have been provided by numerous studies with microbial phytase supplement (Biehl and Baker, 1997; Camden et al., 2001; Kies, et al., 2001; Ravindran et al., 1999, 2000; Sebastian et al., 1997; Yi et al., 1996). These studies generally demonstrated the positive effects of supplemental phytases on the digestibility and utilization of protein and amino acids in broilers as the result of releasing the nutrients from the phytate-bound complexes.

Many studies have demonstrated the improvement of apparent metabolizable energy (AME) from the addition of microbial phytases in diets of poultry (Camden et al., 2001; Kies, et al., 2001; Farrell et al., 1993; Ravindran et al., 2000; Rojas and Scott, 1969). This provided indirect evidences for the interaction of phytate and energy utilization. The increased energy

utilization with added phytase was due, in part, to the increased protein digestibility (Ravindran et al., 2000). It is also possible that added phytase might improve the digestibility of starch and lipids by releasing these nutrients from phytate-complexes (Camden et al., 2000). However, Miles and Nelson (1974) observed that significant improvement of phytase treatment in AME only occurred in birds fed cottonseed meal and not in those fed soybean meal. Ravindran et al. (2000) further observed that the improvement was correlated with the content of non-phytate P.

2.2.3 Environmental Pollution from Unutilized Phytate P in Poultry Farms

As a result of poor utilization of phytate P in poultry, the substantial P in excreta of poultry farms may build up to levels that exceed the requirements of crop production in the adjacent land of intensive poultry farms (Sharpley, 1999). Sims (1997) estimated an annual P surplus of 90-120 kg/ha per years for a typical poultry-grain farm in Delaware, United States. Agricultural runoff (surface and subsurface) and erosion from high P soil may accelerate eutrophication of fresh water (Carpenter et al., 1998; Schindler, 1997). The control of P inputs is critical in reducing freshwater eutrophication (Sharpley, 1999). Eutrophication restricts water use for fisheries, industry and drinking water, due to the increased undesirable algae and aquatic weed and oxygen shortages caused by their death and decomposition. Associated periodic surface blooms of cyanobacteria (blue-green algae) in drinking water supplies may pose a serious health hazard to animals and humans (Sharpley, 1999). A study by Burkholder et al. (1992) demonstrated that *Pfiesteria piscicida*, a small dinoflagellate, was the causative agent of the mortality and morbidity of the major estuarine fish in the eastern areas of the United States and the recent outbreaks was associated the excess nutrients in affected waters. In recent years, the study related to P pollution has gained public attention and subsequently research efforts for

improving the utilization of phytate P in monogastric animals bears an important significance in environmental protection.

2.3. Nutritional Approaches for Improving the Utilization of Phytate

2.3.1 Phytase Supplement

Many fungi, bacteria and yeasts produce phytases which are needed for hydrolysis of phytate to inositol and inorganic phosphorus (Simons et al., 1990). Nelson et al. (1968, 1971) first reported on the addition of microbial phytase to poultry diets. With diets without inorganic P, the birds fed phytase shown a considerable advantage in body bone ash percentage over the controls. Chicks utilized the phytate P hydrolyzed by the phytase as efficiently as they did inorganic P. The enzyme was showed to be active in the gastrointestinal track. Simons et al. (1990) characterized the effects of phytase in-vitro, and verified and extended the results of Nelson et al. (1968). They found that the optimum activity of crude microbial phytase occurred at pH values of 5.5 and 6.5.

In recent studies, the improvement of phytate P from the use of commercial phytase were generally in the range of 20-45% in chicks, and the extent depended on vitamin D, calcium, inorganic and other nutrients in diets (Camden et al., 2001; Kies, et al., 2001; Ravindran et al., 1995).

2.3.2 Addition of Vitamin D isomers

The addition of vitamin D for the improvement of the utilization of phytate P was speculated in some earlier studies. Gillis et al. (1949) observed that high levels of vitamin D_3 improved the performance of chicks fed either calcium phytate or natural phytate P. In a later

study, they found vitamin D_3 caused a small increase in the retention of phytate P^{32} in the bone (Gillis et al., 1957). Matterson (1948) observed that oral administration of large doses of vitamin D caused a marked response in intestinal phytase activity and the increase was accompanied by a decrease in phosphotase activity of the blood. There were extensive reports (Davies et al., 1970; Pileggi et al., 1955) indicating the supplement vitamin D in diets that were low or devoid of vitamin D or some its derivatives increased the level of phytase activity in chickens and rats, and led to some improvement in phytate utilization. Several recent studies indicated that phytate P utilization increased 31%-87% due to the addition of Vitamin D (Edwards, 1993; Mitchell and Edwards, 1996a, b; Mohammed, 1991).

On the other hand, it was also proved that the improvement of utilization of phytate P through the addition of Vitamin D is limited. McGinnis, et al. (1944) found that, even when vitamin D of 320 units per 100 grams was added to the diets that lacked inorganic P, normal bone development could not be obtained in chicks. Furthermore, it was reported that, at an optimum ratio of calcium to available P, little response was obtained from the supplement of vitamin D_3 (Ravindran et al., 1995). Conversely, a response could be obtained if the ration was unbalanced (Nelson, 1976). Recent studies suggested that the optimal condition for the largest effect of vitamin D_3 is the combination of low Ca and low P in the diet (Edwards, 1993; Mitchell and Edwards, 1996a, b; Mohammed et al., 1991).

The effects of vitamin D_3 and microbial phytase in improving the utilization of phytate P in chickens have been shown to be additive. Michell and Edwards (1996) reported that the supplement of 1, 25-$(OH)_2D_3$ in deficient-P broiler diet can replace 0.1% inorganic P, and the combination addition of 1, 25-$(OH)_2D_3$ and phytase can replace 0.2% inorganic P. This amount

nearly equals to the inorganic P supplement added to a normal corn-soybean diet (Michell and Edwards, 1996).

2.3.3 Low Phytate Corn

Two non-lethal phytic acid (***lpa***) mutants of maize have been developed that have 33% (***lpa2***) to 66% (***lpa1***) less phytic acid P in the kernel than normal corn (Raboy and Gerbasi, 1996). These corn hybrids are the same as any normal corn, but the seeds contain considerately lower amounts of phytate P in the germ portion of the kernel, with little effect on total P concentration. Some samples of these corn hybrids contained approximately 0.27% total P and 0.17% available P. In contrast, a near isogenic normal corn contained similar levels of total P but only 0.03% available P (Waldroup, 1999; The author seemly regarded inorganic P as available P). Substitution of the normal corn with low phytate corn can be expected to improve P availability in the diets of poultry and pigs.

There have been studies on nutritional evaluation of low phytate corns in chickens, pigs and turkey (Douglas et al., 2000; Huff et al., 1998; Spencer et al., 2000; Verm et al., 2001; Waldroup, 1999; Yan et al., 2003). It was estimated that the total P content of broiler chicken diets could be reduced at least 11% if diets were prepared with low phytate corn rather than normal corn (Huff, et al., 1998). Compared with the chicks fed diets containing normal corn, the fecal P excretion by chicks fed low phytate diets was reduced by an average of 27.8% and 24.2%, respectively in the cases with and without phytase supplement in the diet (Waldroup, 1999). In corn-soybean type broiler diets, the P content of low phytate corn was 2-3 times more available than the P content of normal corn (Douglas et al., 2000). In pigs, the use of low phytate

corn in the semi-purified and practical pig diets reduced P excretion by 50% and 18.4% respectively compared with the diets containing normal corn (Veum et al., 2001).

2.4. Non-Genetic Factors Affecting the Utilization of Phytate P

Besides exogenous microbial phytase and vitamin D in diets, other non-genetic factors affecting the utilization of phytate P include dietary Ca and P levels, dietary ingredients, processing of feed, and the age of the birds (Ravindran et al., 1995). Phytate P bioavailability is a metric trait in birds. These factors form the nutrition environment for the expression, and influence the genetic properties and the implications in poultry breeding.

2.4.1 Dietary Ca and P

The effects of dietary Ca and P on the hydrolysis of phytate have been well established (Ballam et al., 1984; Edwards and Veltman, 1983; Mohammed, 1991; Nwokolo et al., 1976; Scheideler and Sell, 1987) and were reviewed by Ravindran et al. (1995). Increasing dietary Ca: P ratio was demonstrated to decrease the utilization of phytate P in poultry and narrowing the ratio improved the availability of phosphorus from phytic acid (Harms et al., 1962; Nelson, 1967; Scheidelerm and Sell, 1987; Vandepopuliere, et al., 1961).

2.4.2 Dietary ingredients

It has been long known that some feed ingredients have endogenous phytase activity. Phytases are present in most cereals, but their activity varies widely among cereals (Ravindran et al., 1995). Rye, wheat and barley contain high levels of phytase activity, while corn, oats sorghum and oilseed contain little or none of the enzymes (Ravindran et al., 1995). However, the

phytase activity of plant sources was demonstrated to have a limited role in the hydrolysis of phytate (Ballam et al., 1984; Nelson, 1976).

2.4.3 Processing of feed

Differences exist between phytate forms from different feedstuffs in their response to heat treatment. The destruction of phytate in soybean protein and other feedstuffs has been widely reported (O'Dell, 1962; Kratzer et al., 1959; Summers et al., 1966; Takemasa and Hijikuro, 1991). Summers et al. (1966) further demonstrated that commercial stream pelleting enhanced the utilization of phosphorus in mixed diets. On the other hand, diets containing high levels of steam pelleted wheat product resulted in lower P availability and this reduction was attributed to the destruction of endogenous plant phytase (Summers et al., 1968).

2.4.4 Age of Bird

It is generally thought that older birds hydrolyze phytate P to a greater extent than chicks (Peeler et al., 1972). Maddaiah et al. (1963) demonstrated that mature hens utilized phytate P more efficiently than chicks. Edwards et al. (1989), Aston et al. (1960), and Nelson (1976) also reported that the ability of poultry to utilize phytate P increased with age. However, a contrasting result was reported by Scheideler and Sell (1987). They found that the retention of phytate P was 47% at 34 week, but decreased to 9.1 and 16.5% at 50 and 72 weeks, respectively.

2.5 Variation in the Utilization of Phytate P in Poultry and its Genetic Implication

The study of genetic variability in the utilization of phytate P has been limited. The differences in requirement of P and the response to P-deficient diets among strains may imply

genetic difference in the ability of different strains to utilize phytate P. There has been ample evidence in that endogenous phytase activity exists in the digestion tract of birds (Maenz and Classen, 1998). The activity of some digestive enzymes in poultry has been demonstrated to be related with the selection for body weight (Dunnington et al., 1995; O'sullivan et al., 1992), implying that genetic variance in endogenous digestive enzymes may exist. Consequently, it is reasonable to speculate that differences in endogenous phytases may provide the genetic bases for variation in the utilization of phytate P in growing birds.

2.5.1 The Different Responses of Birds of Different Strains to Phosphorus-Deficient Diets

Earlier investigation on the requirement of phosphorus and the response to graded diet P in chickens were reported about 4 decades ago. Lillie et al. (1964) were not able to demonstrate any difference in P requirement between two broilers strains. In their experiments, graded levels of total P were 0.6, 0.7, 0.8 and 0.9%, of which the added inorganic P levels were 0.23, 0.32, 0.46, and 0.54%, respectively were fed. However, it should be noted that, because 30% plant-sourced phosphorus is generally calculated as available (Scott et al, 1982; NRC, 1994), even the lower levels in the study of the Lillie et al (1964) was close to the P requirement (45% available P) for broilers (NRC, 1994). Gardiner (1969, 1971), using lower graded dietary P levels (0.44, 0.55 and 0.64%), reported a significant interaction between breed and diet P level for body weight, feed consumption, percent bone (4 week), plasma inorganic P and percent livability. However, the largest difference in body weight was between a commercial broiler strain and a Single Comb White Leghorn strain. The causal sources of the interaction were difficult to ascertain. The interaction could be due to the differences in P requirements or the differences in response to P-deficient diets between the two breeds.

Orban and Roland (1990) reported the response of four broiler strains to dietary P above and below the requirements. The four strains were Peterson x Arbor Acres cross, Peterson x Indian River cross, Shaver x Shaver cross and Hubbard White Broiler cross. The basal ration was a typical corn-soybean diet and the grades of dietary available P were 0.14, 0.51 and 0.88% respectively. The strains were evaluated for feed consumption, body weight gain, bone weight, and bone strength. The results showed that there were differences among the strains in these traits at 0.14 % available P, but no difference between strains for all the traits under the diets containing 0.51 or 0.88% available P. The Shaver x Shaver cross was superior to the other 3 strains in all the 4 traits at 0.14 % available P. The interactions of strain and phosphorus were significant ($P<0.05$) for feed consumption, body weigh gain, bone weight and bone strength at the three graded levels of available P.

Zhang et al. (1998) reported the response to P-deficient diets of chicks from two broiler lines selected (11 generations) for high and low incidence of tibial dyschodroplasia (TD). The study demonstrated that chicks did not differ in body weight, mortality and livability, but the control line was significantly superior to the two selection lines in the 3 traits. The control line was had the same population size as the selection lines and in the selection lines, and inbreeding was avoided (Wong-Valle et al., 1993) in each line. Thus, the inferiority of the selected lines to the control line could not be due to inbreeding depression. A possible reason for this contradiction is that, the ability of the chickens to utilize phytate P has not genetic relationship with TD and the difference between the divergent lines in the responses to P-deficient diets might be due to genetic drift occurring in small populations.

Keshavarz (2003) studied the effect of different levels of non-phytate phosphorus (NPP) with and without phytase on the performance of four strains of laying hens. The strains used

were Babcock B300, DeKalb Delta White, Hy-line W36 and ISA-White. The control diets had 0.45% NPP for the entire experiment, and the experimental diets had 0.25-0.15% NPP during different age periods and were supplemented with phyatse in a dose of 300 units per 1 kg diet. The results demonstrated that numerous interactions existed among strain and diet for various traits throughout the experiments. The average daily NPP required for the entire experimental period for maintaining all the production traits (egg production, egg weight, feed conversation, shell weight and others) at the levels close to the corresponding controls was minimal in Hy-Line and, in increasing order, more in Isa-White, DeKalb and Babcock.

2.5.2 The Differences of Retention of Phytate Phosphorus in Birds

Edwards (1983) reported an indirect evidence of the genetic variability in the utilization of phytate P in poultry at population level. He observed that Single Comb White Leghorns were able to utilize suboptimal levels of P in the ration (0.45% total P with 0.32% phytin P) more efficiently than broiler cockerel chickens as measured by growth, livability, and bone calcification. The superiority of the Leghorn-type over the broiler-type in utilizing phytate P at suboptimal levels of P in the diets was accentuated by high levels of calcium in ration. Among broiler strains, the Athens-Canadian randombred cockerels were more efficient than modern commercial broilers in using P at suboptimal levels. The Single Comb White Leghorn showed higher retention values for Ca, P, and phytate P than the broiler strain. Depending on the levels of Ca and P in the diets, the average retention of phytate P in the Single Comb White leghorn strain and the broiler strain ranged 45-56% and 23-37%, respectively.

Smith et al. (1999) studied the genetic variance in chickens of Athens Canadian Randombred strain. They fed 58 mature roasters with a P-deficient diet (0.35% P) and after an acclimatization period of 3 days, the excreta produced in 48 hours ware collected. Five roosters

with lowest excreta P value were categorized as high phytate P utilization sires and five roosters with highest excreta P value were categorized as low phytate P utilization sires. The offspring of high phytate P sires had high body weight and percent bone ash when fed adequate-P diet or suboptimal-P diet, but the excreta phytate values of the offspring at 9-11 days of age had an unexpected negative correlation with the values of their sires. This study implied that the genetic variance within the strain for utilizing phytate P may exist, but may be subject to environmental factors.

At present, there has been not a study in the literature reporting on the genetic basis of phytate phosphorus utilization in poultry. But it can be inferred from the studies of Edwards (1983) and Smith et al. (1999) that genetic variability exists. However, to initiate a marked genetic improvement, an appropriate pedigreed population needs to be established and be subject to selection pressure for several generations, and the environmental effects have to be separated from the phenotypic values.

2.6 Methodology for Genetic Analysis of Population Properties of Metric Traits

2.6.1 Experimental design and Evaluation of Selection Response

Several designs are frequently used in the selection experiments of poultry for removing environmental trends and the resulted fluctuation of phenotypic values, and measuring selection responses. They include establishment of control line(s), divergent selection, and comparison of selected lines (Gowe and Fairfull, 1990). Establishment of control population (s) has been the design of choice for most poultry selection programs. Traditional Least-Square analysis of short-term selection experiments is based on control line (s) to adjust environmental trends for inferring realized heritability (Falconer and Mackey, 1996; Hill, 1990; Walsh, 2004). However,

if the only objective of an experiment is to measure the regression of response on the selection differential, then divergent selection will results in the most efficient use of resources (Falconer and Mackey, 1996). Furthermore, possible asymmetry selection response can be demonstrated from divergent selection (Falconer and Mackey 1996). It should be noted that the use of control populations or divergent selection is not a fool-proved approach for removing environmental trends (Walsh, 2004).

In the mid 1980s, the use of mixed model (MM) methodology in estimating the responses of selection experiments was investigated by Blair and Pollak (1984) and Sorensen and Kenney (1984, 1986). Blair and Pollak (1984) examined the behavior of different estimators of selection response in sheep data. Sorensen and Kenney (1984, 1986) studied properties of MM estimators of selection response through computer simulation. Both studies concluded that MM methods can offer advantages over the traditional least-square techniques. If a number of conditions are satisfied (Henderson, 1975), the MM estimator of selection response partitions the phenotypic trend into its genetic and environmental components, without need a control line (Sorensen and Kennedy, 1986). For traits controlled by a large number of additive loci, the numerator relationship matrix *A* in MM equations accounts for changes in additive genetic variance due to breeding, assortative mating and genetic disequilibrium resulting from selection (Sorensen and Kennedy, 1984). Thus, the methodology is also valid in analyzing a selection experiment of multiple generations. In actual applications, individual breeding values and variance components can be simultaneously inferred with restricted maximum likelihood (REML) or Bayesian methods. Details on the application of MM methodology in the analysis of short selection experiments were described by Kennedy (1990) and Walsh (2004).

There have been numerous reports in the literature on the applications of MM methods in the analysis of the selection response and genetic trend, which was defined as the regression of best linear unbiased prediction (BLUP) estimator of breeding values (EBVs) on generations, in commercial breeding projects and animal selection experiments (Abdallah and McDaniel, 2000; Carcia and Baselas, 2002a,b; Holl and Robison, 2003; Plasse, et al., 2002). In the analysis of poultry selection experiments, mixed model methodology also has been successfully used in removing environmental effects in pooled data of multi-generations and inferring the genetic trends (Bovenhuis et al., 2002; Schulman, et al., 1995; Sewalem et al., 1998).

Schulman et al. (1994) investigated genetic progress in residual feed consumption (RFC) and the related traits in a layer line selected for RFC over four generations. The RCR and body weight gain (BWG) over the period from 16-42 wk of age showed reduction in the last two generations according to BLUP estimated breeding value criterion. But in the term of phenotypic values, the comparison with a control line did not show any change in the selected line for the BWG. Sewalem et al. (1998) studied direct and correlated response in two White Leghorn lines selected for egg number (EN) or egg weight (EW) for 10 generations. They successfully separated environmental effects from the phenotypic values and found that the direct response increased steadily over generations, the EN line had a positive genetic trend for hatchability of fertilized eggs, and EW line had a negative genetic trend for the trait. Bovenhuis et al. (2002) studied the phenotypic and genetic trends in an 18 generation selection experiment of antibody response of chickens to sheep red blood cells. While the genetic trends over generations in the 2 divergent selection lines and a control line were basely consistent with the phenotypic trends, the genetic trend had much smother change profiles than the phenotypic trend, suggesting fluctuation from environmental factors confounded with the stable genetic trend.

Phytate P utilization as a trait is influenced by factors such as: microbial phytase, dietary ingredients, feed processing, Ca and P levels, vitamin D, and age. In a short-term selection project, the phenotypic trends may not indicate the true response to the selection pressure. It is important therefore to use MM methodology with an animal model to analyze selection experiments in order to adequately separate environmental variation from phenotypic values and obtain a correct inference about the genetic change from the selection.

2.6.2 Estimation of Genetic Parameters

The genetic parameters of any given population include heritability and genetic correlation. They play a crucial function in predicting selection response and making breeding schemes (Falconer and Mackey 1996). Genetic parameters are calculated directly from (co) variance components. For metric traits of polygenic inheritance, estimation of genetic parameters is synonymous with the estimation of variance components. It involves a partitioning of observational components, i.e. phenotypic covariance between relatives, into causal components due to additive genetic effects and residual effects (Falconer and Mackay, 1996). Traditionally, this partitioning is completed using analysis of variance (ANOVA) or analogous procedures (Anderson, 1984; Falconer and Mackey, 1996; Henderson, 1953).

Animal breeding data from selection experiments (field records from animal and poultry improvement schemes) is not a random sample. Analysis of ANOVA and the analogous procedures are based on the assumption of random sampling and consequently biased by selection. Furthermore, the genetic information contained in pedigree data cannot be adequately utilized with ANOVA type methods. In contrast, maximum likelihood (ML) methods with an animal model not only can incorporate all known relationship information in the analysis, but

also has a strong robust property and can account for selection under a number of conditions (Kennedy, 1990). Theoretically, it is necessary that all information which has contributed to selection decisions be included in the analysis with ML, unless it is totally uncorrelated to the trait(s) analyzed. However, it has been proved that, even if these conditions are only partially fulfilled, ML estimators are often considerately less biased by selection than their ANOVA counterparts (Meyer, 1989b). Maximum likelihood estimators are consistent, asymptotically normal and efficient (Harville, 1977).

A major drawback of ML estimation is that fixed effects are treated as if they were known, i.e. the loss in degree due to fitting these effects is ignored. Especially, when the loss of degrees of freedom is large relative to the observations, the resulted bias of will be substantial (Verbeke and Molenberghs, 2000). A modified ML procedure, the restricted maximum likelihood (REML) was proposed by Patterson and Thompson (1971). It overcomes this problem by maximizing only the part of likelihood that is independent of the fixed effects. The estimators of REML are still biased, but the bias is much smaller than ML. Furthermore, Gianola and Fernando (1986) also provided a rationale for using REML based on Bayesian approach. It is, when the prior in a Bayesian inference is flat, its mode is the same as in REML. At present, REML has been the standard method for the analysis of variance components. General packages such as SAS and specialized genetic analysis software packages using REML are available (Gilmour et al., 2002; Kackman and Fernando, 2002; Kovaé and Carcì-Cortés, 2002; Meyer, 1989a; Misztal, 1996; Misztal et al., 2002; Shaw, 1987).

Bayesian approach for the estimation of variance components is fundamentally different from the classical frequentist approach (such as ML and REML). In the frequentist approach a parameter is thought to be an unknown, but fixed. In Bayesian approach, a parameter is

considered to be a quantity whose variation can be described by a probability distribution (called prior distribution). This is a subjective distribution, based the experimenter's belief, and is formulated before the data is seen. A sample is taken from a population indexed by the parameter(s) and the prior is updated with this sample information. The updated prior is called posterior distribution (Casella and Berger, 2000). In the actual applications of Bayesian methods with Monte-Carlo Markov Chain (MCMC), we infer a parameter by its sample mean, high posterior density region (HDR) and sample standard deviation (Garthwaite, et al., 2002). This is different from ML or REML, in which we obtain a mode solution as the estimator and the standard error of the estimator is usually obtained with the minus inverse of Fisher's information matrix (Stuard and Ord, 1994; Dodenhoff, et al., 1998).

Gianola and Fernando (1986) advocated the use of Bayesian methods in animal breeding. From the joint distribution, the marginal posterior distribution of an interested parameter is obtained by successively integrating out all parameters, which include the fixed effects, the additive genetic merits, and variance components. This integration is difficult by analysis or numerical means, and approximations are required. Monte-Carlo Markov Chain procedures brought a breakthrough for obtaining the marginal distribution. One of these procedures, Gibbs sampling, has been extensively studied in statistics.

The applications of Bayesian methods with MCMC in the analysis of animal breeding data started in early 1990's (Sorensen et al., 1994, 1995; Wang et al., 1993; Wang et al., 1994). The theories and procedures have been summarized (Sorensen and Gianola, 2001). Furthermore, several software packages have been developed, making Bayesian approach a main competitor of REML for addressing various problems in animal genetics, including breeding value estimation, decomposition of variance components and quantitative trait loci analysis

(Duangjinda et al., 2001; Thaller and Hoeschele, 1996a,b; Van Kaam et al., 2002; Van Tassel and Van Vleck, 1996).

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CHAPTER 3

GENETICS OF PHYTATE PHOSPHOROUS BIOAVAILABILITY: HERITABILITY AND GENETIC CORRELATIONS WITH GROWTH AND FEED UTILIZATION TRAITS

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ABSTRACT

The current study was undertaken to estimate variance components for phytate phosphorus bioavailability (PBA) and the genetic correlations among PBA and 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 in 3 consecutive days were collected and feed consumed (FC) measured. Individual 4-wk BW and BW gain (BWG) during the period of 3 days for excreta collection 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 correlation 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 suggesting 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.

3.1 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 has 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 the strain of bird, age, ingredient type, and dietary levels of calcium (Edwards, 1983), inorganic phosphorus (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 differences 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 body weight 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 phytate P bioavailability (PBA) and genetic correlations of PBA with growth and feed utilization (or intake) traits.

3.2 Materials and Methods

Birds

The data were collected on an unselected random mating Athens-Canadian Randombred (ACRB) chicken population (Hess, 1962). Twenty-six randomly selected sires were mated to 71 randomly selected dams (sex ratio 1:2~3) to hatch 1,004 chicks in 6 hatches at 7 d intervals. Chicks were placed in pens with litter and fed corn and soybean meal type diets until 4 wks of age. From hatch till 2 wks of age, a diet containing 3.20 Kcal/kg ME, 23% crude protein (CP), 1.0 % Ca, 0.74% total P and 0.24% inorganic P. From 3-4 wk the birds were fed a diet that contained 3.20 Kcal/kg ME, 20% protein, 0.90% Ca, and 0.68% total P, and 0.32% inorganic P. At 4 wk of age, birds were transferred to individual metabolism cages and fed the same diet with the mineral source of P largely removed and calcium and total P adjusted to 1.06 and 0.35% respectively. After a 3 d period of acclimatization, excreta produced on 3 consecutive d were collected and feed consumed (FC) measured. Individual 4-wk BW and BW gain (BWG) during the 3 d excreta collection period were also measured. Excreta were oven-dried at 80^{o}C and

ground. Phytate P in the feed and dried excreta was determined by method described by Latta and Eskim (1980). The disappearance of phytate during the 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:

PBA = (A- B)/A × 100%

A = phytate P content in feed (%) × feed intake (g)

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 Statistics 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:

$$Y_{ijk} = u + S_i + H_j + SH_{ij} + e_{ijk}$$

where Y_{ijk} is the individual observation for a trait, u is the overall mean, S_i is the sex effect (i=1,2), H_j is hatch group effect (j=1,2..6), SH_{ij} is the interaction effect of sex and hatch group, and e_{ijk} is the individual total random effect. Individuals with trait data beyond 3 standard deviations from the estimated sample mean were considered as outliers and consequently removed from the data set. After data editing, 901 individuals with complete data sets from 26 sires and 71 dams, and 105 grandparents (44 males and 61 females) 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, were calculated by subtracting the least square estimates for the fixed effects from the observed values.

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

$$y = X\beta + Zu + e$$

where, $y = (y_1' \quad y_2' \ldots y_t')'$ 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' is the vector of fixed effects for trait *t*; $u = (u_1', u_2' \ldots u_t')'$ and u_t' is vector of random animal effects for trait *t*; $e = (e_1', e_2' \ldots e_t')'$ and e_t' is the vector of residual effects for trait *t*. The variances of random animal effects were $var(u) = A \otimes G$ and $var(e) = I \otimes R$, where A is the additive relationship matrix, G is the (co)variance matrix for genetic effects of the traits, I is the identity matrix and R is the (co)variance matrix for the corresponding residual effects. For a univariate model, G and R are σ_a^2 and σ_e^2 respectively, in a scalar form.

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 Henderson (1975) and Quaas (1976) methods. 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

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

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

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

where $\text{var}(\hat{\theta})$ 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 $SE(h^2)$, $\theta = [\sigma_a^2 \ , \ \sigma_e^2 \ ]'$.

3.3 Results and Discussion

The means, standard deviation, coefficient of variation, and minimum and maximum values for the traits measured are listed in Table 3.1. The range of PBA is consistent with the observations of Edward (1983). The variability in PBA was about 24%. The ANOVA results of the fixed model showed that there were differences (P<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 variance 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*<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 3.1. The normal Q-Q plot (Figure 3.2) of TRE shows that the distribution had no apparent departure from normality. Both Figures 3.1 and 3.2 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 indicate that the assumptions $y \sim N(X\beta,\ V)$ for REML methodology were met in variance component estimation for PBA.

The estimates of variance components and heritability for measured traits are listed in Table 3.2. The heritability of PBA from both the univariate and multivariate models was about 0.10 and the standard error for the estimate was small. This demonstrates that there is 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 was 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 sub-optimal 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 new genetic parameter estimation may be required. Analysis of variance with TRE showed that there were no sex differences for PBA, and consequently a heritability value (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 heritability 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 in the 3 d excreta sampling period at 4 wk of age. The short duration of the test period may 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 3.3. The phenotypic correlations between PBA and BW, BWG, FC, and FCR were low. Phenotypic correlations among growth and feed related traits were consistent with literature 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 indicating 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 antagonist relationship between growth and PBA may 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 compared to 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 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 will not adversely affect FCR, at least for the ACRB population. The genetic relationship between growth and feed related traits have been discussed extensively in literature (see Chambers, 1990). The current study is the first of its kind reporting on the genetics of PBA and its relationship with growth. A comprehensive relationship between PBA, growth, and feed related traits and reproductive capacity is needed before any breeding strategy 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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TABLE 3.1. Means, SD, CV, and range of phytate P bioavailability (PBA), BW (4 wk), BW gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) in 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

TABLE 3.2. 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) in a 3 d period in a random mating control population of chickens.

Trait	LSMEAN±SE		Variance Components[1]		
	Male (n=435)	Female (n=466)	$\sigma_A^2 \pm SE$	$\sigma_e^2 \pm SE$	$h^2 \pm SE$
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	105.80 ± 8.08	0.38 ±0.06
FCR (g:g)	2.34 ± 0.02[a]	2.37 ± 0.02[b]	0.01 ± 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<0.05).

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

TABLE 3.3. 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	

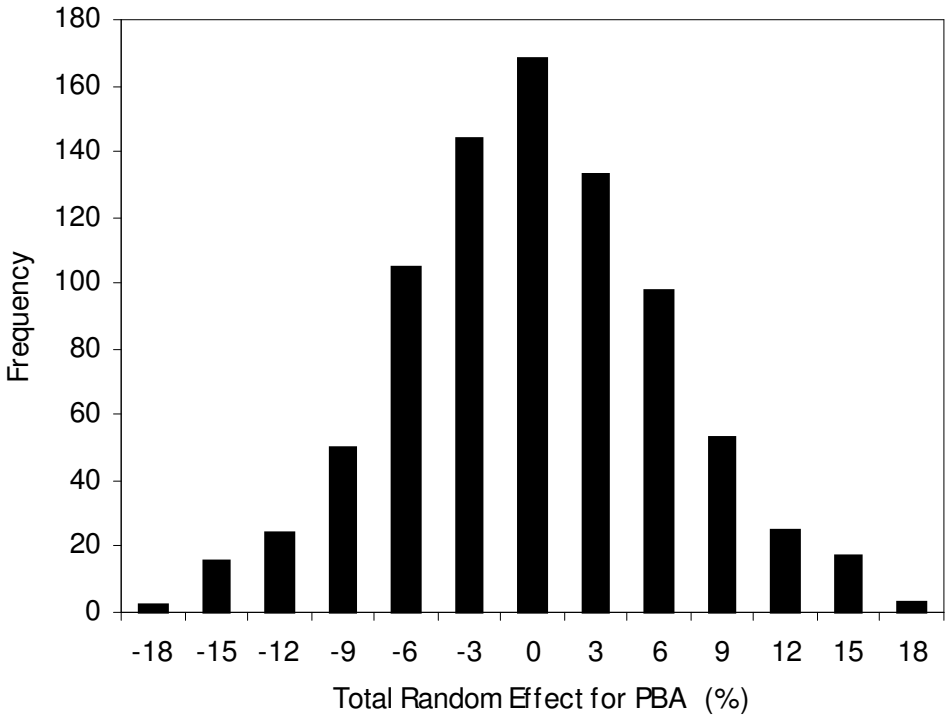

FIGURE 3.1. The distribution of the total random effect (additive genetic effect + residual) of phytate P bioavailability in a control chicken population of chickens.

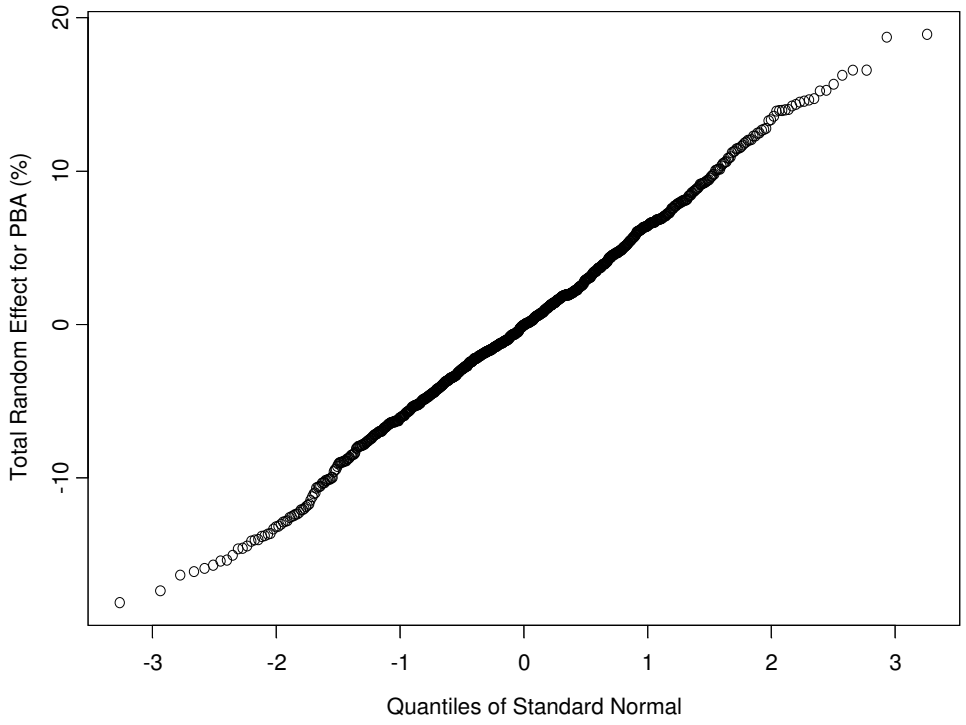

FIGURE 3.2 The normal Q-Q plot for the total random effect (additive genetic effect + residual) of phytate P bioavailability in control population of chickens.

CHAPTER 4

GENETIC ANALYSIS ON THE DIRECT RESPONSE TO DIVERGENT SELECTION FOR PHYTATE PHOSPHORUS BIOAVAILABILITY

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ABSTRACT

This study was undertaken to evaluate the direct response to a 3-generation divergent selection for phytate phosphorus bioavailability (PBA) in Athens-Canadian Randombred (ACRB) population of chickens. Cumulated divergent response (R_C), which was calculated as the line difference in PBA after adjusting for hatch and sex effects, were used to assess the direct selection response. The results showed a significant response at generation 1 (G_1). The R_C was unchanged from G_1 to G_2 and had an increase (1.62%) from G_2 to G_3 ($P<0.01$) due to the application of best linear unbiased prediction (BLUP) selection in H-line at G_2.

The average BLUP estimated breeding value (EBV) was employed to determine the genetic trend for the selected trait across generations. The results showed that the genetic trend was symmetric at G_1 and G_2, but asymmetric at G_3. The application of mixed model methodology was effective in separating environmental component from the phenotypic change. When the data of H-line or L-line in the selected generations (G_1 - G_3) was combined with the data of the base population (G_0), the heritability estimates for PBA were 0.07 ± 0.02 and 0.09 ± 0.02, respectively, which were higher than the realized heritability (.03-.06).

The H-line and L-line both showed significant increases or decreases in the average BLUP EBVs across the generations. This demonstrates that modest progress can be obtained by incorporating PBA into selection programs. However, other correlated traits of economic importance need to be evaluated before any such decision to incorporate selection of PBA into breeding schemes should be initiated.

4.1 Introduction

The traditional genetic model for quantitative traits is the infinitesimal model, under which a trait is assumed to be controlled by many unlinked additive genes of small effect, and allele frequencies and Mendelian sampling variance are not subject to selection (Bulmer, 1985; Fisher, 1918). However, the model is not always valid. Several studies have demonstrated that selection can cause changes in the additive genetic variance of typical metric traits (Beniwal et al., 1992; Heath et al., 1995). This makes the prediction of selection responses of multiple generations based on genetic parameters invalid in some practical applications. Thus, there are many consequences of selection that can only be discovered through experiments (Falconer and Mackay, 1996).

The utilization of phytate phosphorus is of economic importance in poultry because of the obvious nutritional cost and environmental implications (Ravindran et al., 1995). Genetic variance for phytate P bioavailability (PBA) has been estimated in the Athens-Canadian Randombred (ACRB) population (Chapter 3, this dissertation). From the genetic parameter estimates, it was suggested that PBA could be improved through a genetic approach. However, other genetic properties of the trait are still unknown.

In order to ascertain the feasibility of the genetic improvement in PBA, a divergent selection of PBA was initiated in the ACRB population for 3 generations. The measurement of PBA is not without error. There are various sources of variation that are confounded in the estimation of PBA. As the result, a least square analysis based on the comparisons between the divergent lines may be not effective in the term of detecting the genetic changes in each line.

Mixed model (MM) methodology has proven to be an optimal approach for analyzing selection experiments (Kennedy, 1990). With an animal model, the gene flow is traced over

generations, environmental trend is removed, and the best linear unbiased prediction (BLUP) estimators of breeding values (EBV) and selection response are obtained. In poultry, applications have been reported (Bovenhuis et al., 2002; Schulman et al., 1994; Sewalem et al., 1998).

The objective of current study was to evaluate the direct response to selecting for low and high PBA. The cumulated divergent response (R_C) was first investigated with a fixed effect model. The MM methodology with an animal model was used to infer the genetic trends of the selected trait (PBA). The variance components and heritability of the trait were estimated using several pooled data sets in order to further clear the genetic properties.

4.2 Material and Methods

4.2.1 Birds and selections

Thirty-five sires and 105 dams randomly selected from Athens-Canadian Randombred (ACRB) were used to generate the base population (G_0) and each sire was randomly arranged to mate with 3 females through artificial insemination. The phytate P bioavailability of the population has been described in Chapter 3 (this dissertation). Birds were ranked according to their hatch-corrected PBA values to establish the divergent sub-populations.

Divergent Selection: For the high PBA line (H-line), 18-22 males and 40-46 females with the highest hatch-corrected PBA values were selected as breeder candidates. For the low PBA line (L-line), 18-22 males and 40-46 females with the lowest hatch-corrected PBA values were selected as breeder candidates. However, at generation 2, the breeder candidates for the H-line were selected on their BLUP EBV values rather than their phenotypic values. From the breeder candidates, 12 males and 36 females that had normal performance in meeting artificial

insemination (AI) and egg collection requirements were randomly selected as the actual breeders for each line. One sire was mated to 3 dams by AI, and sibling mating was avoided whenever possible. The direct selection for PBA was performed for 3 generations. About 900 individuals in the base generation and 430 individuals per line in generations 1 to 3 were used in the analysis. The number of offspring of all sires and dams was well balanced. The selection differentials and intensities are listed in Table 4.1.

4.2.2 Experimental methods

At each generation, the experimental birds were reproduced in 6 hatches with an interval of 7 days. Chicks were placed in pens with litter and fed corn and soybean meal type diets until 4 wk of age. From hatch until 2 wks of age, a diet containing 3.20 Kcal/kg ME, 23% crude protein (CP), 1.0 % Ca, 0.74% total P and 0.24% inorganic P. From 3-4 wk the birds were fed a diet that contained 3.20 Kcal/kg ME, 20% protein, 0.90% Ca, and 0.68% total P, and 0.32% inorganic P. At 4 wk of age, the birds were transferred to individual metabolism cages and the mineral source P in the ration was largely removed such that Ca and total P was adjusted to 1.06 and .35% respectively, and other nutrients were maintained at the same levels as in the diet for the birds of 3-4 wk. After an acclimatization period of 3 days, the excreta produced in 3 consecutive days were collected. Excreta collected were oven-dried at 80^0C and ground. Phytate in the feed and dried excreta was determined by the method described by Latta and Eskim (1980). The disappearance of phytate during the passage of feed through the total tract was considered as the indicator of phytate P utilization (Ravindran et al., 1995). Phytate P bioavailability (PBA) was estimated as follows:

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

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

4.2.3 Statistics Analysis

The PROC GLM (SAS Institute, 1998) was used to analyze the effects of sex, hatch group and line (for G_1-G_3). The cumulated divergent response (R_C) was evaluated with the following model:

$$Y_{ijkl} = L_i + S_j + H_k + LS_{ij} + e_{ijkl}$$

where L_i = line effect (i=1,2), S_j = sex effect (j=1,2), H_k = hatch group effect (k=1,2….6), LS_{ij} = the interaction of line and sex. Y_{ijkl} = individual PBA values, and e_{ijkl} = residual. For G_0, terms L_i and LS_{ij} were not included. Records with student residual greater than 3 standard deviations for PBA were considered as outliers and were removed. After data editing, 891 completed records in G_0, 707 completed records in G_1, 672 completed records in G_2, and 658 completed records in G_3 were used for obtaining descriptive statistics (SAS Institute, 1998). The pooled data were used to obtain the BLUP estimated breeding values (EBV) with mixed model techniques. In addition, 97 parents and 105 grandparents of G_0 were included in the analysis.

Cumulated divergent responses (R_C) were calculated as the differences of the least square means of the phenotypic values of PBA between H-lines and L-line after sex and hatch effects were adjusted. Genetic trends were calculated by regressing average EBV on generation for each line (Schulman, 1995; Bovenhuis et al., 2002; Carcia and Basela, 2002). Realized heritability (h_r^2) of PBA was obtained by regressing EBV on cumulated selection differential across generations for each line (Blair and Pollak, 1984; Kennedy, 1990).

A univariate mixed linear model (Henderson, 1984) was fitted to obtain the best linear unbiased prediction (BLUP) of additive genetic effects of individuals across generations for PBA and to estimate the heritability for the base population. Three pooled data sets were used in the estimation of heritability and they included: (1) whole data across generations and lines, (2) the data of G_0 and G_1- G_3 in H-line, (3) the data of G_0 and G_1- G_3 in L-line. Heritability was calculated according to the definitions (Falconer and Mackay, 1996). The standard errors were based on the asymptotic variances of $f(\hat{\theta}_t)$ (Stuard and Ord, 1994; Dodenhoff et al, 1998).

The general expression of a univariate mixed model is

$$y = X\beta + Zu + e$$

where, **y =** the vector of observations; **X =** matrix that relates fixed effects to records; **Z =** matrix that relates animals to the records; β **=** the vector of fixed effects; **u =** vector of random animal effects (or additive genetic effects); **e =** the vector of residual effects. The variances of random effects were **var(u) =A** σ_a^2 and **var(e) = I** σ_e^2**,** where **A** is additive relationship matrix, **I** is an identity matrix, σ_a^2 is the additive genetic variance of the traits, and σ_e^2 is the residual variance.

Generations and hatches within generations were combined into 24 generation-hatch groups (GH). Sex and hatch group were included in the model as fixed effects. The formation of $\mathbf{A^{-1}}$ was based on Henderson's (1975) and Quaas's (1976) methods. The calculation of BLUP and variance components was accomplished using average information algorithm for REML (Johnson and Thomson, 1995) with AiREML program (Misztal et al., 2002). Convergence was considered to have been reached when

$$\| \hat{\theta}_t - \hat{\theta}_{t-1} \|^2 / \| \hat{\theta}_t \|^2 < 5 \times 10^{-11}$$

where $\hat{\theta}_t$ is the vector of estimated parameters in t iteration, and the Delta convergence was lower than 5×10^{-6}.

4.3 Results and Discussion

The descriptive statistics of PBA in generations1-3 are listed in Tables 4.2. The cumulated divergent responses (DR_C) in PBA are shown in Figures 4.1. In general, the means of PBA fluctuated over generations. There was not sexual dimorphism ($P<0.05$). The comparisons (Table 4.3) between lines demonstrated a small divergent response ($R_C = 0.94 \pm 0.50$, $P<0.05$) after one generation of selection (at G_1). The R_C remained unchanged fromG_1 to G_2. There was an increase by 1.62% from G_2 to G_3 ($P<0.01$).

The descriptive statistics of BLUP estimated breeding values (EBV) of PBA at G_0 - G_3 are summarized in Table 4.4. The differences of EBV between H-line and L-line were similar to the phenotypic responses (DR_C) (Table 4.3). The genetic trends were symmetric at G_1 and G_2, but the profile was apparently asymmetric at G_3 (Figure 4.2). From G_2 to G_3, the average EBV in the L-line decreased only 0.35%. The corresponding increase in the H-line was 0.82%. This asymmetry was due to the different criteria in the selection of breeders at G_2, where the criterion was the hatch-corrected phenotypic value in L-line and the BLUP of individual breeding values in the H-line. The rationale for this argument can be found in a simulation study by Belonsky and Kennedy (1988). The study showed that BLUP selection gave 55-80% greater response than individual phenotypic selection for a trait of low heritability.

The regression coefficients of the average EBV on the generations were 0.50 and -0.29 in the H-line and L-line and they were both significant ($P<0.05$). The estimates of the heritability and genetic variance of PBA using different pooled data sets are listed in Table 4.5. When only

the data of G_0 and G_1 - G_3 in the H-line was used, the estimated additive genetic variance and heritability were 3.47 ± 0.96 and 0.07 ± 0.02 (E2). When only the data of G_0 and G_1 - G_3 in the L-line was used, the estimates were 3.92 ± 1.08 and 0.09 ± 0.02 (E3). The two sets of estimates were close to each other and consistent with the estimates obtained using data of the base population exclusively (see Chapter 3). This suggested that the estimation of heritability of the trait was not subject to the selection and an additive model of many loci would be appropriate for the genetic analysis (Bulmer, 1985; Kennedy, 1990; Sorensen and Kennedy, 1984).

However, the combination of the data of the divergent lines led to a lower estimate of additive genetic variance in E1 (Table 4.5). This may be attributed to the experimental errors and assortative mating in establishing the divergent lines from the base population. A simple explanation is provided here and the verification requires a simulation study. Compared with the residual variance component, the additive genetic variance of PBA was small, and consequently two individuals with the same genotype may have very different phenotypic values. Suppose there were two full-sibs A and B in G_0, and their hatch-corrected phenotypic values of PBA were 20% and 40%, respectively. In establishing the divergent lines, A would be selected as a sire or dam in H-line and would be arranged to mate with bird(s) that had high additive genetic value(s) with a high probability, and consequently its progeny would have higher genetic values. On the contrary, B would be selected as a sire or dam in L-line and would be arranged to mate with bird(s) that had low additive genetic value(s) with a high probability, and consequently its progeny would have lower genetic values. Thus, the offspring of A would lack resemblance with the offspring of B. As the result, resemblance between relatives was maintained within a line and was partially lost between lines. Genetic variance is determined by the resemblance between

relatives. Therefore, the loss of resemblance between relatives in the combined data set would result in the decrease of the estimated genetic variance.

The realized heritability (h_r^2) of PBA was calculated to be 0.06 ± 0.02 and 0.03 ± 0.01 for the H- and L- lines, respectively. Although they were smaller than the estimated heritability (0.09 ± 0.03) for the base population (see Chapter 3), the true realized heritability may be even lower than 0.06. At G_2, BLUP selection was used in the H-line. This would fast the genetic improvement, leading an overestimate of h_r^2. However, the inconsistence of h_r^2 and h^2 does not means h^2 was over-estimated.

The mixed model approach with an animal model has been highly advocated for the analysis of selection experiments (Kennedy, 1990; Walsh, 2004). In this study, the application proved to be effective in the separation of observed change into its environmental and genetic components. However, the prediction of genetic trends from BLUP EBV was still limited in accuracy. This was suggested by the low correlation ($r_{a\hat{a}}$) between the BLUP estimated breeding values and the true breeding values. This correlation is also called empirical accuracy (Meyer, 1989) and can be generally calculated according to the following equations (Henderson, 1984; Mrode, 1996).

$$r_{a\hat{a}} = \sqrt{\frac{\mathrm{var}(\hat{a})}{\mathrm{var}(a)}} \qquad \mathrm{var}(\hat{a}) = \mathrm{var}(\hat{a} - a)$$

In the current study, the estimated additive genetic variance ($\mathrm{var}(a)$) for the base population with the whole pooled data was 2.36, and the corresponding standard deviation of BLUP of breeding values ($\sqrt{\mathrm{var}(\hat{a})}$) was 0.75, and consequently $r_{a\hat{a}}$ was 0.49. The empirical accuracy is similar to published results (Meyer, 1989). According to Meyer (1989), for a trait with

heritability of 0.25, $r_{a\hat{a}}$ values generally were below 0.8 except for the sires with large number of progenies.

In summary, the efficacy of divergent selection for PBA was evaluated for 3 generations. The results indicated that the phenotypic values of PBA were influenced by environmental factors and as a result the response to selection was erratic across generations. However, when the environmental factors were separated from the phenotypic values, the H-line and L-line both showed significant increase or decrease in PBA EBVs across the generations. This demonstrates that modest progress can be obtained by incorporating PBA into selection programs. However, other correlated traits of economic importance need to be evaluated before any such decision to incorporate selection of PBA into breeding schemes should be initiated.

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Table 4.1 Selection differential and intensity for phytate P bioavailability (PBA) at different generations[1,2,3]

	Selection Differential (%)		Selection Intensity	
	H-Line	L-Line	H-Line	L-Line
Generation 0 (G_0)				
Male	9.88	10.12	1.54	1.57
Female	10.61	10.51	1.65	1.59
Average	10.25	10.32	1.60	1.59
Generation 1 (G_1)				
Male	9.70	8.31	1.48	1.27
Female	7.61	6.97	1.61	1.06
Average	8.66	7.64	1.32	1.17
Generation 2 (G_2)				
Male	8.79 (1.09[4])	10.02	1.41	1.61
Female	1.67 (0.65)	4.66	0.25	0.74
Average	5.23 (0.87)	7.43	0.83	1.17

[1] At G_0, the selection differentials were calculated as the differences between means of the breeders and the means of whole population.

[2] At G_1 and G_2, the selection differentials were calculated as the differences of the means of the breeders and the means of the corresponding line sub-populations.

[3] For H-line at G_2, the selection was based on BLUP values of additive genetic effects.

[4] Average BLUP estimated breeding value estimated with the data of H-line sub-population at G_2.

Table 4.2 Descriptive statistics of phytate phosphorus bioavailability (PBA, %) for a 3-generation divergent selection program

	Generation 1 (G_1)					Generation 2 (G_2)					Generation 3 (G_3)				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
H-M	187	30.97	7.51	7.37	56.87	165	33.47	6.85	17.57	58.43	166	30.45	7.82	7.22	56.23
H-F	172	29.22	7.72	7.04	54.10	160	32.74	6.67	17.66	55.00	191	31.25	8.42	9.21	55.27
L-M	186	28.93	7.25	6.56	46.44	165	32.14	5.70	17.06	46.75	167	28.12	8.09	6.23	57.77
L-F	170	29.86	7.17	6.56	48.09	168	32.11	5.44	19.59	45.25	166	28.13	9.04	5.23	54.66

H-M males in H-line; H-F females in h-line; L-M males in H-line; L-F females in L-line.

Table 4.3 Last square means of phytate phosphorus bioavailability (PBA, %) in the divergent selection lines and the cumulated divergent response (DR_C).

	H-line	L-line	DR_C ($\hat{\theta} \pm SE$)
Generation 1 (G_1)	30.29	29.34	$0.94 \pm 0.50^{*}$
Generation 2 (G_2)	33.09	32.11	$0.97 \pm 0.47^{*}$
Generation 3 (G_3)	30.76	28.20	$2.55 \pm 0.63^{**}$

* $P<0.05$; ** $P<0.01$

Table 4.4 Best linear unbiased prediction (BLUP) estimated breeding values (EBVs) for phytate P bioavailability (PBA, %) across generations

[1]Generation: Line	N	Mean	SD	Min	Max
G_0	894	-0.01	0.75	-2.28	2.36
G_1: H-line[2]	360	0.40	0.77	-1.41	2.72
$G_{1:}$ L-line	355	-0.45	0.70	-2.50	1.29
G_2: H-line	325	0.80	0.69	-0.67	3.07
G_2: L-line	333	-0.59	0.46	-2.42	0.72
G_3: H-line	357	1.62	0.55	0.46	3.35
G_3: L-line	333	-0.94	0.64	-2.56	0.86

[1] G_0- G_3: Generations 0-3.

[2] H-line: High PBA line L-line: Low PBA line

Table 4.5 Estimation of variance components and heritability (h^2) of phytate P bioavailability (PBA) using different data sets ($\hat{\theta} \pm SE$) with a univariate model.

	[4]σ_A^2	[5]σ_E^2	h^2
[1]Estimation 1 (E1)	2.34 ± 0.53	44.68 ± 0.92	0.05 ± 0.01
[2]Estimation 2 (E2)	3.47 ± 0.96	43.91 ± 1.23	0.07 ± 0.02
[3]Estimation 3 (E3)	3.92 ± 1.08	41.08 ± 1.23	0.09 ± 0.02

[1] Estimated using the whole pooled data;

[2] Estimated using the data of G_0 and G_1- G_3 in H-line;

[3] Estimated using the data of G_0 and G_1- G_3 in L-line;

[4] Additive genetic variance component;

[5] Residual variance component.

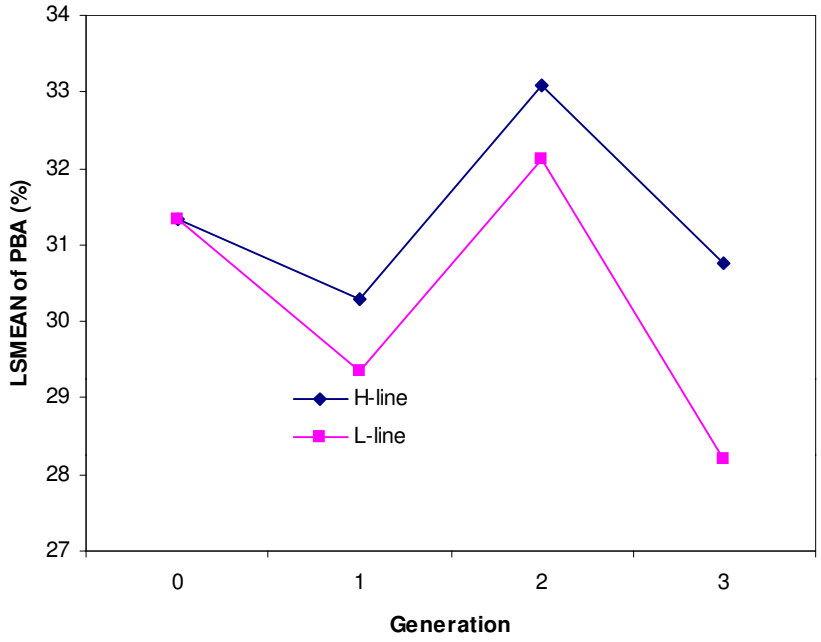

Figure 4.1 Phenotypic trends of phytate P bioavailability (PBA) in the divergent line.

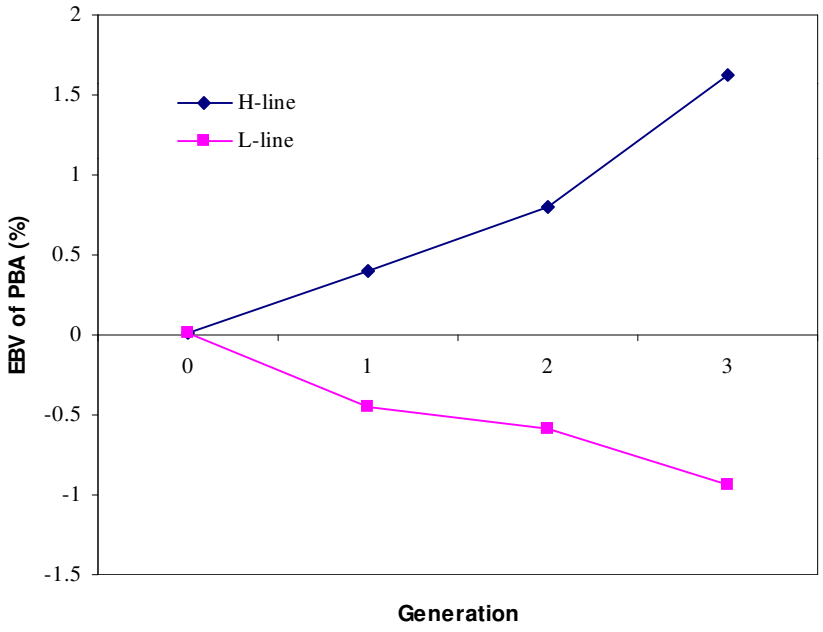

Figure 4.2 Genetic trends of phytate P bioavailability (PBA) in the divergent lines.

CHAPTER 5

GENETIC ANALYSIS ON THE CORRELATED RESPONSES TO DIVERGENT SELECTION FOR PHYTATE PHOSPHORUS BIOAVAILABILITY

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ABSTRACT

This study was undertaken to evaluate the correlated response to a divergent selection of 3 generations for phytate phosphorus bioavailability (PBA) in Athens-Canadian Randombred (ACRB) population of chickens. The studied traits included body weight at 4 weeks of age (BW), BW gain (BWG), feed consumption (FC), and feed conversion ratio (FCR) during a period of 3 days. The first employed evaluation criterion was DCR_C (cumulated divergent correlated response), which was calculated as the line difference of the least square means of phenotypic values for each trait at a indicated generation after sex and hatch effects were adjusted. The results showed a consistent correlated response in BW across generations. The DCR_C at generation 3 (G_3) was 26.8 g ($P<0.01$). The chickens in the low PBA line (L-line) had higher BW than the high PBA line (H-line). The DCR_C in BWG, FC and FCR was significant ($P<0.05$) only at G_3.

The second evaluation criterion was the average best linear unbiased prediction (BLUP) estimated breeding value (EBV), which was employed for separating environmental effects from phenotypic values in order to infer the genetic trends for the correlated traits across generations. The results showed asymmetric genetic trends in BW, BWG, and FC, and the correlated responses were mainly due to the genetic changes that occurred in H-line, and little genetic change occurred in L-line across generations. FCR did not show any genetic trend. At G_3, the line differences of EBV were close to the DCR_C values for all the traits except FCR. This suggested that DCR_C and EBV criteria would tend to be consistent with the increase of generations. However, at G_1 and G_2, the line differences of the EBV actually deviated from the DCR_C values for BWG and FC. The inconsistency could be attributed to experimental errors that were not accounted by the fixed model for obtaining DCR_C. The genetic correlations of PBA

with BW, BWG and FCR that were observed in the base population (G_0) became much weaker when the information of the selected generations (G_1 - G_3) was combined with the data of G_0 for the estimation, and the genetic correlations were different for the divergent lines. This suggests the genetic covariance was subject to the selection. The underlying mechanism is still not clear. A possible explanation for the asymmetric correlated responses could be involved in the pleiotropic effects of major gene(s) on PBA and the correlated traits.

5.1 Introduction

A quantitative trait is assumed to be affected by many genes. As the result of pleiotropy, the same sets of genes can control more than one trait. The strength of the relationship between traits controlled by the same sets of genes can be measured by the genetic correlations among the traits. When selection pressure is applied to a trait, there would be an according genetic change in the correlated trait(s), depending on the selection intensity and the genetic correlations between them. The correlated responses from selection for goal trait(s) are important in livestock breeding and experimental study, and have been frequently investigated in all kinds of farm animals and poultry (Garcia and Baselga, 2002; Fredeen and Mikami, 1986; Kaplon et al., 1991; Katle and Kolstad, 1991; Kuhlers and Jungst, 1993; Schulman et al., 1994; Tufvesson et al., 1999).

Phytate phosphorus utilization is a trait of economic importance in poultry because of its obvious nutrition cost and environmental implications (Ravindran et al, 1995). Genetic selection is a potential approach for the improvement of phytate phosphorus utilization in poultry (Aggrey et al., 2002; Zhang et al., 2003). The genetic basis for the trait has been investigated (Zhang et al., 2003). Negative relationship between phytate phosphorus bioavailability (PBA) and growth rate was implied by previous study (Edwards, 1983) and verified in a recent study (Zhang, et al, 2003). A modest but significant response was observed from a short-term divergent selection for PBA (Chapter 4, this dissertation).

In this study, the cumulated divergent correlated responses (DCR_C) in body weight (BW), BW gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) to the divergent selection for PBA and the genetic trends of these traits were investigated. The genetic

correlations (r_A) of the selected trait with the related traits were estimated with several pooled data sets in order to infer the effect of selection on the genetic covariance.

5.2 Material and Methods

5.2.1 Birds and selections

Thirty-five sires and 105 dams randomly selected from Athens-Canadian Randombred (ACRB) were used to generate the base population (G_0) and each sire was randomly arranged to mate with 3 females through artificial insemination. The PBA, and growth and feed utilization performance characteristics of the base population have been reported in Chapter 2. Birds were ranked according to their hatch-corrected PBA values to establish the divergent sub-populations.

Divergent Selection: For the high PBA line (H-line), 12 males and 36 females from individuals with highest hatch-corrected phenotypic values were selected as breeders. For the low PBA line (L-line), 12 males and 36 females from individuals with the lowest hatch-corrected PBA values were selected as breeders. At generation 2, the breeder candidates in H-line were selected on their BLUP EBV values rather than their phenotypic values. Within each line, one sire was mated to 3 dams by artificial insemination. The direct selection for PBA was performed for 3 generations. At each generation, about 430 individuals per line were measured (see section 5.2.1).

Correlated traits: The correlated traits measured at each generation were BW at 4 wk, BWG, FC and FCR. Details of the measurement will be described in 5.2.2.

5.2.2 Experimental methods

At each generation, the experimental birds were reproduced in 6 hatches with an interval of 7 days. Chicks were placed in pens with litter and fed corn and soybean meal type diets until 4

wk of age. From hatch until 2 wks of age, a diet containing 3.20 Kcal/kg ME, 23% crude protein (CP), 1.0 % Ca, 0.74% total P and 0.24% inorganic P. From 3-4 wk the birds were fed a diet that contained 3.20 Kcal/kg ME, 20% protein, 0.90% Ca, and 0.68% total P, and 0.32% inorganic P. At 4 wk of age, the birds were transferred to individual metabolism cages and the mineral source P in the ration was largely removed such that Ca and total P were adjusted to 1.06 and .35% respectively, and other nutrients were maintained at the same levels as in the diet for the birds of 3-4 wk. After an acclimatization period of 3 days, the excreta produced on 3 consecutive days were collected.

Individual body weights at 4 week of age (BW), and body weight gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) during the excreta collection period of 3 days were measured. FCR was calculated as the ratio of FC with BWG. Excreta collections were oven-dried at 80^0C and ground. Phytate in the feed and dried excreta was determined with the method described by Latta and Eskim (1980). The disappearance of phytate during the passage of feed through the total tract was considered as the indicator of phytate P utilization (Ravindran et al., 1995) and phytate P bioavailability (PBA) was estimated as follows:

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

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

5.2.3 Statistics Analysis

The PROC GLM (SAS Institute, 1998) was used to test the effects of sex, hatch group and line (for G_1-G_3), find the outliers in the data set for each generation, and evaluate the cumulated divergent correlated response (DCR_C). The full model was

$$Y_{ijkl} = L_i + S_j + H_k + LS_{ij} + e_{ijkl}$$

where L_i = line effect (i=1, 2), S_j = sex effect (j=1,2), H_k = hatch group effect (k=1,2….6), LS_{ij} = the interaction of line and sex. Y_{ijkl} = individual observation for a trait and e_{ijkl} = residual. For G_0, terms L_i and LS_{ij} were not included. Records with student residual greater than 3 standard deviations for PBA and the correlated traits were considered as outliers and were removed. After data editing, 891 completed records in G_0, 707 completed records in G_1, 672 completed records in G_2, and 715 records with completed information for BW4, BWG, FC and FCR in G_3 were used for obtaining descriptive statistics (SAS Institute, 1998). The pooled data set was used in the estimation of breeding values with mixed model techniques. In addition, 97 parents and 105 grandparents of G_0 were included in the analysis.

Cumulated divergent correlated responses (DCR_C) were calculated as the differences of the least square means of the phenotypic values of traits between H-lines and L-line at the indicated generation after sex and hatch effects were adjusted. Genetic trends were calculated by regressing average estimated breeding values (EBV) on generations for each line (Bovenhuis et al., 2002; Carcia and Basela, 2002; Schulman et al., 1985).

A multivariate mixed linear model (Henderson, 1984; Mrode,1996) was fitted to obtain the best linear unbiased prediction (BLUP) of additive genetic effects of individuals of all generations for BW4, BWG, FC and FCR. Corresponding to each generation and each line, the means of the BLUP value was obtained as average EBV.

Bivariate mixed models were fitted to estimate the genetic correlations of the correlated traits with PBA and a univariate mixed model was used to estimate the heritability for the base population. Three pooled data sets were used in the analysis, which included: (1) whole pooled data across generations and lines, (2) the data of G_0 and G_1- G_3 in H-line, (3) the data of G_0 and

G_1- G_3 in L-line. Genetic parameters were calculated according to the definitions (Falconer and Mackay, 1996). The standard errors were based on the asymptotic variances of $f(\hat{\theta}_t)$ (Stuard and Ord, 1994; Dodenhoff et al., 1998).

The general expression of a mixed model was

$$y = X\beta + Zu + e$$

where, **y =** ($\mathbf{y}_1'$ $\mathbf{y}_2'$ ..... $\mathbf{y}_t'$)' and $\mathbf{y}_t'$ is the vector of observations for trait **t**; **X =** matrix that relates fixed effects to records; **Z =** matrix that relates animals to the records; $\beta = (\beta_1', \beta_2' ... \beta_t')'$ and β_t' is the vector of fixed effects for trait **t**; **u =** ($\mathbf{u}_1'$ $\mathbf{u}_2'$ ..... $\mathbf{u}_t'$)' and $\mathbf{u}_t'$ is vector of random animal effects (or additive genetic effects) for trait **t**; **e =** ($\mathbf{e}_1'$ $\mathbf{e}_2'$ ..... $\mathbf{e}_t'$)' and $\mathbf{e}_t'$ is the vector of residual effects for trait **t**. The variances of random effects were **var(u) = A** $\otimes$ **G** and **var(e) = I** $\otimes$ **R,** where **A** is additive relationship matrix, **G** is the (co)variance matrix for genetic effects of the studied traits, **I** is an identity matrix and **R** is the (co)variance matrix for the corresponding residual effects.

Generations and hatch groups within generations were combined into 24 generation-hatch groups (GH). Sex and GH were included in the model as fixed effects. The formation of $\mathbf{A^{-1}}$ was based on Henderson's (1975) and Quaas's (1976) methods. The calculation of BLUP and variance components was accomplished using average information algorithm for REML (Johnson and Thomson, 1995) with AiREML program (Misztal, et al., 2002). Convergence was considered to have been reached when

$$\| \hat{\theta}_t - \hat{\theta}_{t-1} \|^2 / \| \hat{\theta}_t \|^2 < 5 \times 10^{-11}$$

where $\hat{\theta}_t$ is the vector of estimated parameters in t iteration, and the Delta convergence was lower than 5×10^{-6}.

5.3 Results and Discussion

5.3.1 Cumulated divergent correlated responses (DCR_C)

The descriptive statistics of BW, BWG, FC and FCR in generations1-3 and the fixed model analysis are listed in Tables 5.1 – 5.4. The DCR_C in BW, BWG, FC, and FCR to the divergent selection for PBA are shown in Figures 5.1. – 5.4, respectively. In general, the means of the traits fluctuated over generations. The comparisons (Table 5.5) between lines demonstrated a small DCR_C ($P<0.05$) in BW (-5.8 g) after one generation of selection (at G_1), and the L-line had higher BW than the H-line. After 3 generations of selection, the DCR_C in BW had reached -26.8 g ($P<0.01$). The DCR_C in BWG, FC and FCR were not significant at G_1 and G_2 ($P>0.05$). However, after 3 generations of selection, there were significant DCR_C in BWG ($P<0.01$), FC ($P<0.01$) and FCR ($P<0.05$). The H-line had lower BW, BWG, FC and higher FCR, compared with the L-line. The DCR_C showed a trend across the generations in FC. However, the trends in BWG and FCR were not clear.

5.3.2 Divergence of EBV and genetic trends

The descriptive statistics of BLUP estimated breeding values (EBV) of BW, BWG, FC and FCR at G_0 - G_3 for the high and low PBA lines are summarized in Tables 5.6- 5.7, respectively. The differences of EBV for these traits between H-line and L-line were similar to the phenotypic responses (DCR_C) (Tables 5.5). The line differences of EBV for BW increased across the generations. However, the line difference for FC only occurred at G_2 and G_3 and for BWG only at G_3. For FCR, there was a small line difference in EBV at G_1 and G_2, and the difference was nearly zero at G_3. From Table 5.6 - 5.7 and Figure 5.5-5.8, it can be observed that the EBV for all traits did not fluctuate as their phenotypic values in both H-line and L-line. The

EBV for BW, BWG and FC genetically tended to decrease in H-line and almost kept unchanged in L-line. It seems that the differences between lines for these traits were mainly due to the changes of EBV that occurred in the H-line.

The regression coefficients of the average EBV on generations were -8.01, -0.80, -2.01, and 0.00, for BW, BWG, FC, and FCR, respectively in the H-line. Among all the traits, only BW in the H-line had a significant slope ($P<0.05$). Similarly, the regression coefficients were -0.506, -0.136, -0.096, and 0.00 for BW, BWG, FC, and FCR, respectively in the L-line. None of the regression coefficients in the L-line were significantly different from zero ($P>0.05$).

5.3.3 Estimation of genetic parameters of the related traits using pool data sets.

The heritability (h^2) and the genetic correlations (r_A) of BW, BWG, FC and FCR estimated with different pooled data sets are listed in Table 5.8 and Table 5.9, respectively. E1 was estimated using the whole data set across lines and generations. E2 was estimated using the data of G_0 and G_1 - G_3 in H-line. E3 was estimated using the data of G_0 and G_1 - G_3 in L-line. The heritability of BW and FC and FCR was consistent in E1-E3. The negative genetic correlations of PBA with BW and FC were stronger in E2 than in E3, and the values in E1 were between E2 and E3. The negative genetic correlations between FCR and PBA were high in all the three estimations. The genetic correlation between PBA and BWG was positive (0.24 ± 0.14) in E3, however, this correlation was zero and very low in E1 and E2, respectively.

The phenotypic data exhibited fluctuations across generations and still had not formed a trend after the selection of three generations. This was due to the influence of environmental factors, such as feed ingredients, ground feces and temperatures. It also means that, in a short-term selection project when genetic progress is relatively small compared with the environmental

effects, we cannot expect to infer from the phenotypic trend of a trait for each line, and the evaluation of the correlated responses should be determined from the line comparison and the estimation of breeding values.

When a comparison of the values at G_3 was made, we found the differences of the EBV between H-line and L-line were close to the DCR_C values for BW, BWG and FC. They were -23.86 (g) vs. -26.80 (g) for BW; -4.02 (g) vs. -3.40 (g) for BWG; -5.85 vs. -4.98 g for FC. But at G_1 and G_2, the line differences of EBV deviated from the DCR_C values for BWG and FC. The inconsistence could be attributed to experimental errors that were not accounted by the fixed model for obtaining DCR_C. This also means the least-square (LS) analysis based on line comparisons sometimes can not indicate the true genetic changes occurred in a short-term selection project (Kennedy, 1990; Walsh, 2004).

For FCR, the line differences of EBV were distinguishable from the FCR values at all the three generations. Furthermore, a clear trend of FCR for both from DCR_C and EBV criteria could not be ascertained. This implies that in the short-term, selection for PBA did not affect feed efficiency. This result was suggested by the small genetic correlations between PBA and FCR estimated with the records of the base population, was not in concordance with the high negative genetic correlation between them estimated with the pooled data sets.

Theoretically, we can establish simple linear equations by regressing EBV on generations for predicting the genetic trends of the related traits (Falconer and Mackey, 1996; Walsh, 2004). But in this study, the selections was undertaken only for 3 generations, and the genetic changes were relatively small and not stable for most traits, and consequently only the equation for BW in H-line had a significant slope coefficients ($P<0.05$). Therefore, data from more generations of selection will be needed for establishing useful prediction equations.

The profile of the genetic correlations of PBA and the correlated traits estimated using the different pooled data set did not follow any pattern. In the estimation using the data of the base population exclusively, the genetic correlations of PBA with BW, BWG and FC were negative and moderate (Chapter 3, this dissertation). This was in concordance with genetic trends in both the H- and L- lines. However, when information of the selected generations (G_1 - G_3) was combined, the relationship tended to become weaker, even reversed in direction, and showed line dimorphism.

In the estimation (E2) using the combined data of G_0 and H-line, the genetic correlation between PBA and BW was moderately negative and this was consistent with the genetic trends in H-line. In the estimation (E3) using the combined data of G_0 and L-line, the genetic correlation between PBA and BW was almost negligible and this was consistent with the lack of genetic changes in L-line. A similar phenomenon was observed for FC.

The genetic correlation between PBA and BWG in the estimations using pooled data sets (E1-E3) was unexpected and not in concordance with the genetic trend profile. The selection showed a negative genetic trend in H-line, yet the genetic correlation was negligible in the estimation (E2) using the combined data of G_0 and L-line. The high negative genetic correlation between PBA and FCR in E1-E3 is difficult to interpret. It seems that the genetic covariance of PBA and FCR was unstable because their genetic variances were small and their measurement was subject to substantial errors in the short term experiment.

Currently there is no adequate theory about the influence of selection on genetic covariance. The mechanism underlying the inconsistent estimates of genetic correlations using different data sets is still not clear. The unknown mechanism could be the underlying factors

behind the asymmetric correlated responses in BW, BWG and FC. A possible explanation for the asymmetric correlated responses could be involved in the pleiotropic effects of major gene(s).

Some major genes have modest effects on the associated metric traits, and do not significantly influence the distribution profiles of the phenotypic and genetic values when the frequencies were low. For example, a recessive and sex-linked dwarfing allele dw^B in poultry was found to be associated with only 10% body weight deduction, smaller than a standard deviation (Shiva Prasad and Jaap, 1977). Therefore, while we have demonstrated (Chapter 3, 4) that the inheritance of PBA was not apparently deviated from an additive model of many loci, it was still possible that a recessive allele(s) with a "large effect" and a low frequency in the base population controlled the trait besides other genes with small effect. The pleiotropic effects of the allele(s) may be associated with high PBA and low growth rate. This would be a main contributory factor for the moderately negative genetic correlations of PBA with BW, BWG and FC, which were estimated using the data of the basic population exclusively. When we selected PBA, the frequency of the allele(s) would increase in the upward line, leading to the according indirect responses in the correlated traits. Meanwhile, in the downward line, the rate at which the frequency of the allele(s) decreased would be slow (due to the recession of the alleles in heterozygotes), and, as the results, the growth and feed utilization traits would keep unchanged in the alteration of generations.

In summary, from this investigation it can be inferred that direct selection for PBA can consequently led to concurrent changes in BW, BWG, FC, and FCR in the high line, however, similar changes in the low line was less appreciable.

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Table 5.1 Descriptive statistics of body weight at 4 week of age (BW, g) in a 3-generation divergent selection program for phytate P bioavailability (PBA)

	Generation 1 (G_1)					Generation 2 (G_2)					Generation 3 (G_3)				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
H-M	187	319.64	41.61	192.40	443.30	165	305.15	50.85	188.40	425.80	171	317.02	49.12	196.60	443.30
H-F	172	283.21	30.04	183.50	390.00	162	269.92	41.65	173.00	376.50	197	268.30	48.07	134.60	431.50
L-M	186	323.50	40.99	212.40	423.70	173	312.53	40.52	200.00	420.80	172	343.29	49.23	195.50	455.30
L-F	170	292.45	37.14	143.00	385.30	170	276.76	38.42	175.70	359.80	173	296.16	44.52	152.10	411.80

H-M males in H-line; H-F females in h-line; L-M males in H-line; L-F females in L-line.

Table 5.2 Descriptive statistics of body weight gain (BWG, g) during the period of metabolism experiment (3 days) in a 3-generation divergent selection program for phytate P bioavailability (PBA)

	Generation 1 (G_1)					Generation 2 (G_2)					Generation 3 (G_3)				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
H-M	187	57.47	14.52	28.60	108.30	165	53.33	10.42	21.70	78.40	171	52.06	10.69	30.40	86.50
H-F	172	49.36	12.72	26.40	96.40	162	43.77	9.17	21.50	77.70	197	44.62	10.69	20.10	85.80
L-M	186	56.54	14.77	25.90	114.40	173	52.65	8.32	32.70	78.50	172	56.00	9.76	32.50	84.70
L-F	170	50.91	12.76	27.70	101.40	170	43.82	9.22	19.80	70.50	173	47.26	10.78	21.60	83.30

H-M males in H-line; H-F females in h-line; L-M males in H-line; L-F females in L-line.

Table 5.3 Descriptive statistics of feed consumption (FC, g) during the period of metabolism experiment (3 days) in a 3-generation divergent selection program for phytate P bioavailability (PBA)

	Generation 1 (G_1)					Generation 2 (G_2)					Generation 3 G_3)				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
H-M	187	115.59	16.11	72.20	158.40	165	123.56	18.86	67.90	162.40	171	124.57	18.91	66.60	177.00
H-F	172	102.49	13.39	62.10	144.40	162	106.73	14.43	52.20	150.00	197	108.25	20.03	60.59	158.30
L-M	187	113.53	16.02	81.40	157.60	173	122.07	15.01	79.90	164.30	172	129.30	17.54	84.50	165.30
L-F	170	102.09	14.13	70.50	143.00	170	106.43	15.05	62.90	144.20	173	112.13	18.22	63.01	155.50

H-M males in H-line; H-F females in h-line; L-M males in H-line; L-F females in L-line.

Table 5.4 Descriptive statistics of feed conversion ratio (FCR, g:g) during the period of metabolism experiment (3 days) in a 3-generation divergent selection program for phytate P bioavailability (PBA)

	Generation 1 (G_1)					Generation 2 (G_2)					Generation 3 (G_3)				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
H-M	187	2.10	0.42	1.11	3.34	165	2.36	0.35	1.31	3.71	171	2.45	0.41	1.26	3.73
H-F	172	2.17	0.46	1.20	3.22	162	2.50	0.39	1.37	3.48	197	2.50	0.48	1.05	3.71
L-M	186	2.09	0.41	1.19	3.28	165	2.35	0.28	1.55	3.29	172	2.35	0.35	1.34	3.54
L-F	170	2.09	0.43	1.14	3.40	170	2.48	0.34	1.45	3.61	173	2.44	0.41	1.58	3.61

H-M males in H-line; H-F females in h-line; L-M males in H-line; L-F females in L-line

Table 5.5 Cumulated divergent correlated response (DCR_C) in body weight (BW), body weight gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) to the divergent selection for phytate phosphorus bioavailability (PBA)[1] .

Traits	Generation 1 (G_1)	Generation 2 (G_2)	Generation 3 (G_3)
BW (g)	-5.76 ± 2.87	-7.37 ± 3.32	-26.80 ± 3.49
BWG (g)	-0.07 ± 0.99	0.25 ± .71	-3.40 ± 0.75
FC (g)	1.52 ± 1.05	0.71 ± 1.17	-4.98 ± 1.24
FCR (g/g)	0.04 ± 0.03	0.02 ± 0.03	0.08 ± 0.03

[1] DCR_C was calculated as the differences of the least square means of phenotypic values for each trait between high PBA line and low PBA line after sex and hatch effects were adjusted.

Table 5.6 BLUP estimated breeding values (EBVs) for body weight (BW) at 4 weeks, and body weight gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) across generations in the line selected for high phytate P bioavailability (PBA).

Trait	Mean	SD	Min	Max
		G_0 (N=894)		
BW4 (g)	-1.32	23.94	-81.31	90.65
BWG (g)	-0.58	3.82	-11.08	13.35
FC (g)	-0.84	6.77	-23.10	22.32
FCR (g/g)	0.01	0.08	-0.23	0.35
		G_1 (N=359)		
BW4 (g)	-4.33	25.36	-78.52	68.08
BWG (g)	-0.23	4.07	-11.64	12.74
FC (g)	0.68	6.91	-22.58	16.92
FCR (g/g)	0.00	0.06	-0.22	0.18
		G_2 (N=327)		
BW4 (g)	-11.60	27.50	-73.16	62.58
BWG (g)	-.88	4.16	-14.09	10.31
FC (g)	-2.33	7.57	-24.88	17.36
FCR (g/g)	0.01	0.08	-0.17	0.24
		G_3 (N=368)		
BW4 (g)	-25.56	27.39	-109.93	58.58
BWG (g)	-3.04	4.50	-14.19	9.22
FC (g)	-6.54	8.07	-28.04	16.15
FCR (g/g)	0.02	0.08	-0.13	0.30

Table 5.7 BLUP estimated breeding values (EBVs) for body weight (BW) at 4 weeks, and body weight gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) across generations in the line selected for low phytate P bioavailability (PBA).

Trait	Mean	SD	Min	Max
		G_0 (N=894)		
BW4 (g)	-1.32	23.94	-81.31	90.65
BWG (g)	-0.58	3.82	-11.08	13.35
FC (g)	-0.84	6.77	-23.10	22.32
FCR (g:g)	0.01	0.08	-0.23	0.35
		G_1 (N=356)		
BW4 (g)	2.20	23.75	-52.05	64.26
BWG (g)	-0.30	4.23	-8.77	11.71
FC (g)	0.46	6.64	-14.93	17.05
FCR (g:g)	0.03	0.07	-0.14	0.22
		G_2 (N=343)		
BW4 (g)	-1.72	27.70	-54.82	56.65
BWG (g)	-1.14	3.56	-10.83	9.97
FC (g)	-0.98	6.65	-17.85	17.30
FCR (g:g)	0.03	0.06	-0.15	0.29
		G_3 (N=345)		
BW4 (g)	-1.70	25.33	-77.36	61.52
BWG (g)	-0.99	3.87	-9.90	8.10
FC (g)	-0.69	8.02	-21.50	21.52
FCR (g:g)	0.02	0.05	-0.06	0.17

Table 5.8 Genetic correlations (r_A) and residual correlations (r_E) of phytate phosphorus bioavailability with body weight (BW) at 4 weeks, and body weight gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) estimated using different pooled data sets.

Related Traits	[1]Estimation 1 (E1)		[2]Estimation 2 (E2)		[3]Estimation 3 (E3)	
	r_A	r_E	r_A	r_E	r_A	r_E
BW	-.21 ± 0.01	-.12 ± .03	-.30 ± .12	07 ± .04	-.06 ± .12	-.15 ± .05
BWG	.00 ± 0.12	.08 ± .02	.03 ± .15	.10 ± .01	.24 ± .14	.04 ± .03
FC	-.18 ± 0.12	.08 ± .02	-.35 ± .13	-.02 ± .02	-.10 ± .13	-.05 ± .03
FCR	-.45 ± .14	-.13 ± .01	-.46 ± .15	-.12 ± .01	-.35 ± .14	-.11 ± .02

[1] Estimated using the whole pooled data;

[2] Estimated using the data of G_0 and G_1- G_3 in H-line;

[3] Estimated using the data of G_0 and G_1- G_3 in L-line.

Table 5.9 Genetic variance (σ_A^2)and heritability (h^2) of body weight (BW) at 4 weeks, and body weight gain (BWG), feed consumption (FC) and feed conversion ratio (FCR) estimated using different pooled data sets.

Related Traits	[1]Estimation 1 (E1)		[2]Estimation 2 (E2)		[3]Estimation 3 (E3)	
	σ_A^2	h^2	σ_A^2	h^2	σ_A^2	h^2
BW	1080.89 ± 78.62	.58 ± .03	1114.03 ± 84.27	.60 ± .03	1003.51 ± 94.82	.57 ± .04
WG	32.35 ± 8.12	.27 ± .06	31.61 ± 7.68	.26 ± .06	30.41 ± 10.16	.26 ± .08
FC	92.75 ± 13.44	.41 ± .05	85.40 ± 13.68	.38 ± .05	94.02 ± 16.21	.43 ± .06
FCR	0.01 ± .00	.08 ± .02	0.02 ± .00	.09 ± ..01	0.01 ± .00	.09 ± .02

[1] Estimated using the whole pooled data;

[2] Estimated using the data of G_0 and G_1- G_3 in H-line;

[3] Estimated using the data of G_0 and G_1- G_3 in L-line.

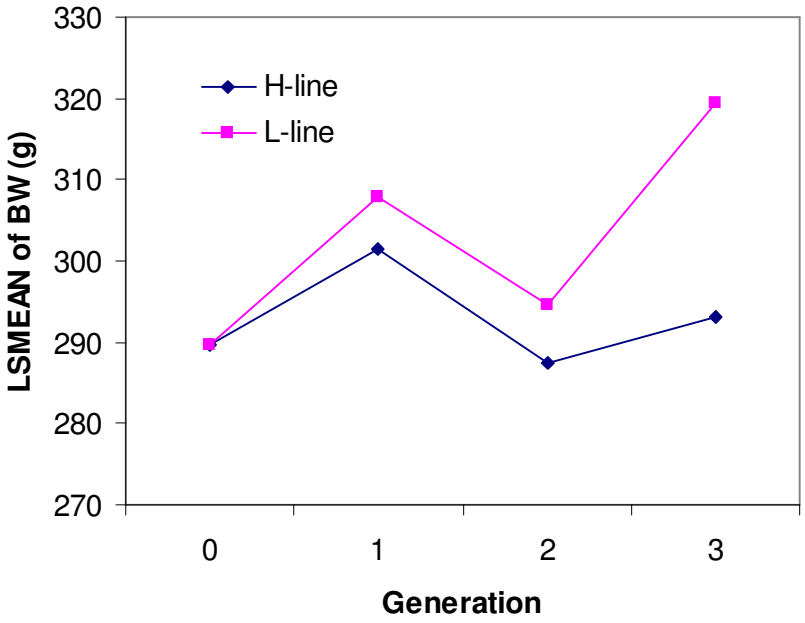

Figure 5.1 Correlated responses in body weight at 4 weeks (BW) to the divergent selection for high or low phytate P bioavailability (PBA).

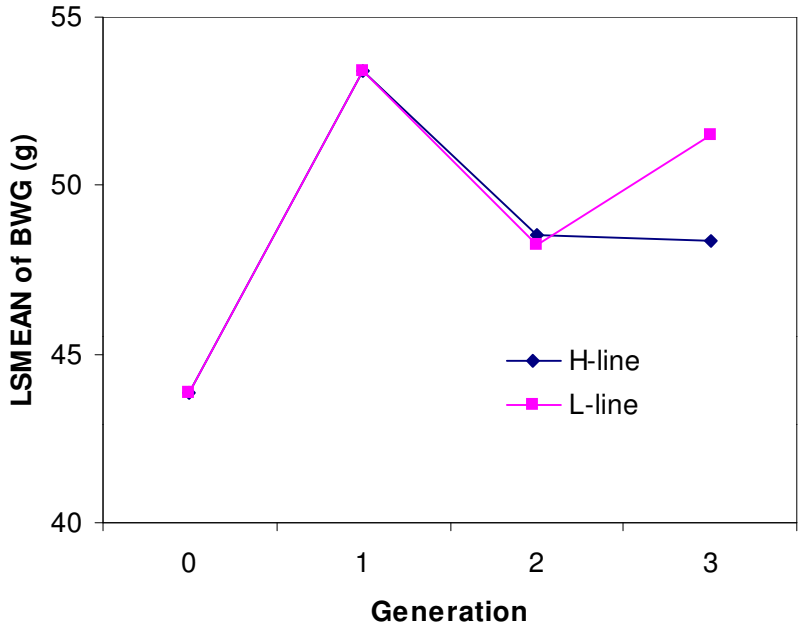

Figure 5.2 Correlated responses in body weight gain (BWG) to the divergent selection for high or low phytate P bioavailability (PBA).

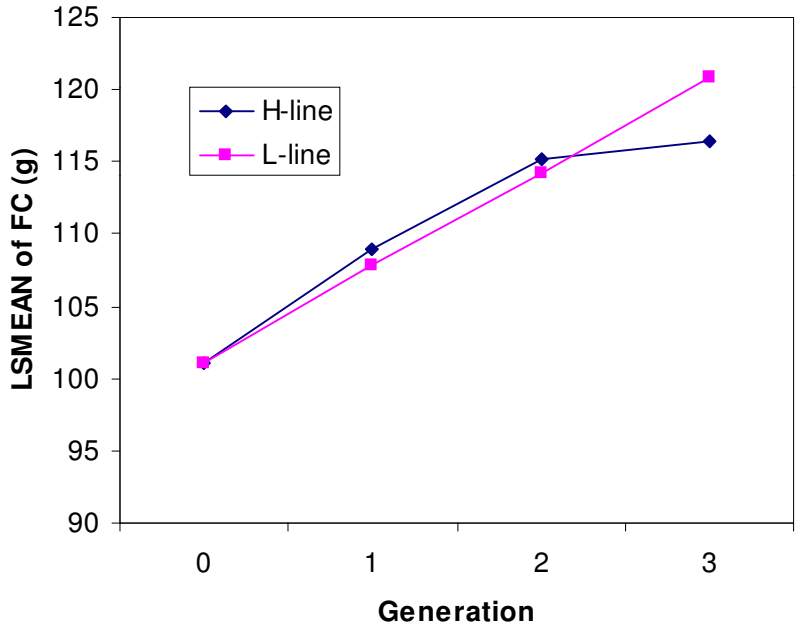

Figure 5.3 Correlated responses in feed consumption (FC) to the divergent selection for high or low phytate P bioavailability (PBA).

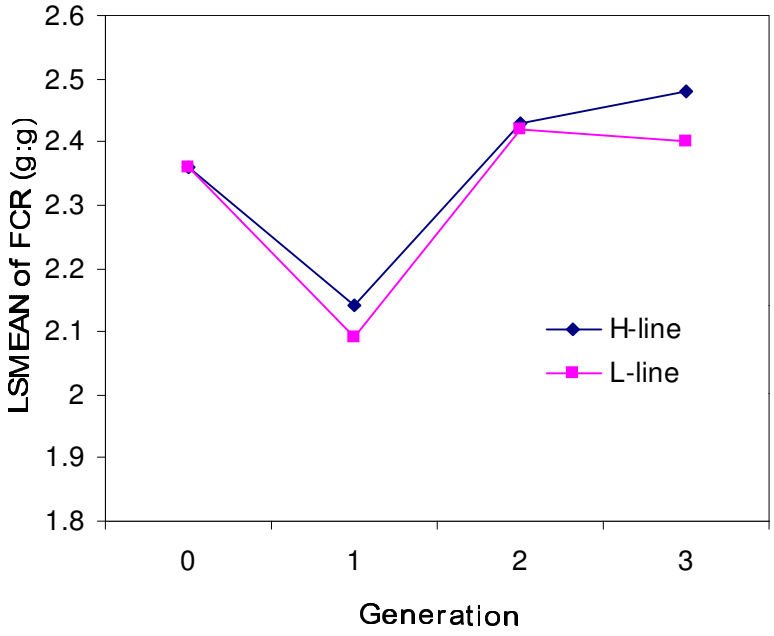

Figure 5.4 Correlated responses in feed conversion ratio (FCR) to the divergent selection for high or low phytate P bioavailability (PBA).

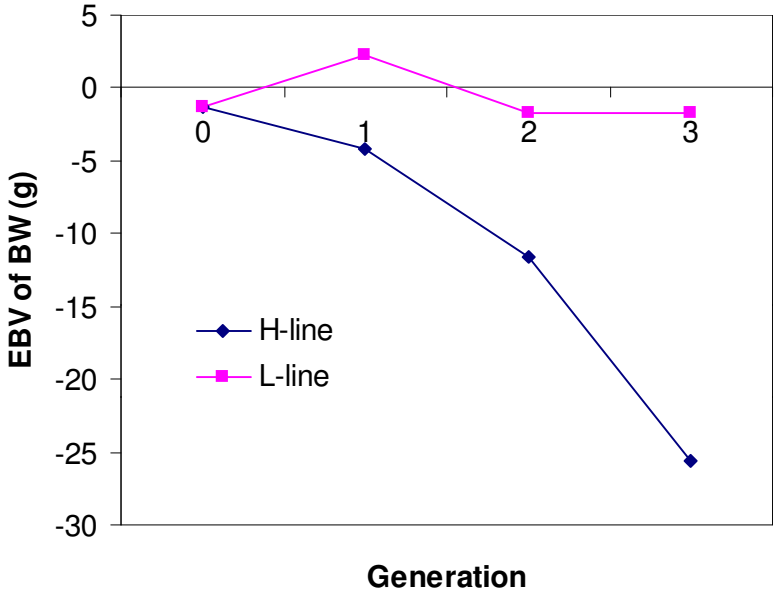

Figure 5.5 Genetic trends of body weight at 4 weeks (BW) in the divergently selected lines for high or low phytate P bioavailability (PBA).

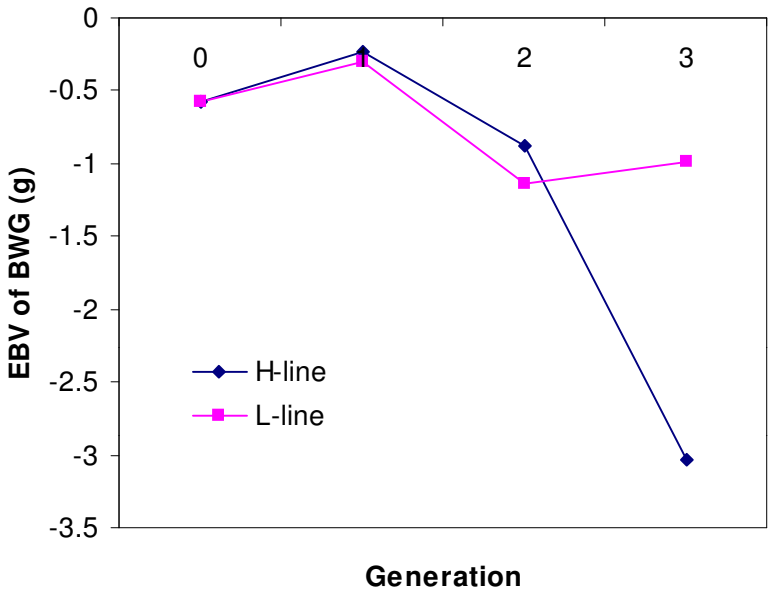

Figure 5.6 Genetic trends of body weight gain (BWG) in the divergently selected lines for high or low phytate P bioavailability (PBA).

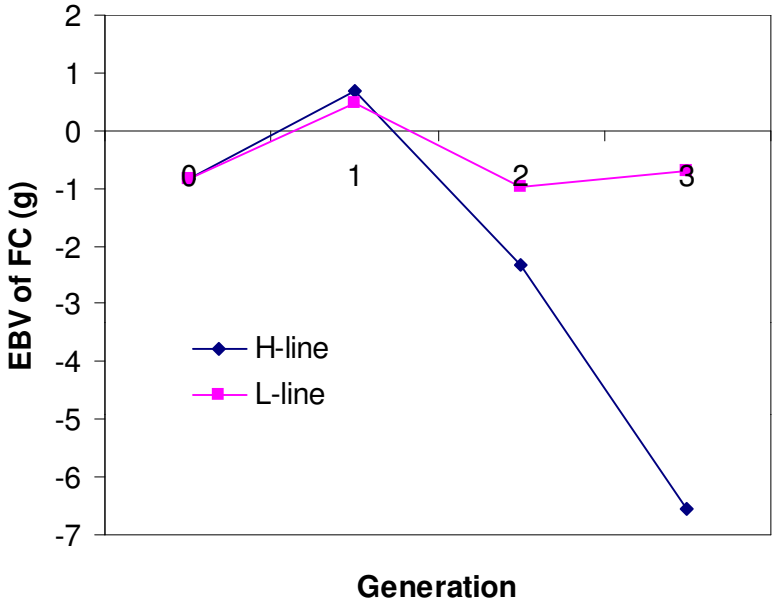

Figure 5.7 Genetic trends of feed consumption (FC) in the divergently selected lines for high or low phytate P bioavailability (PBA).

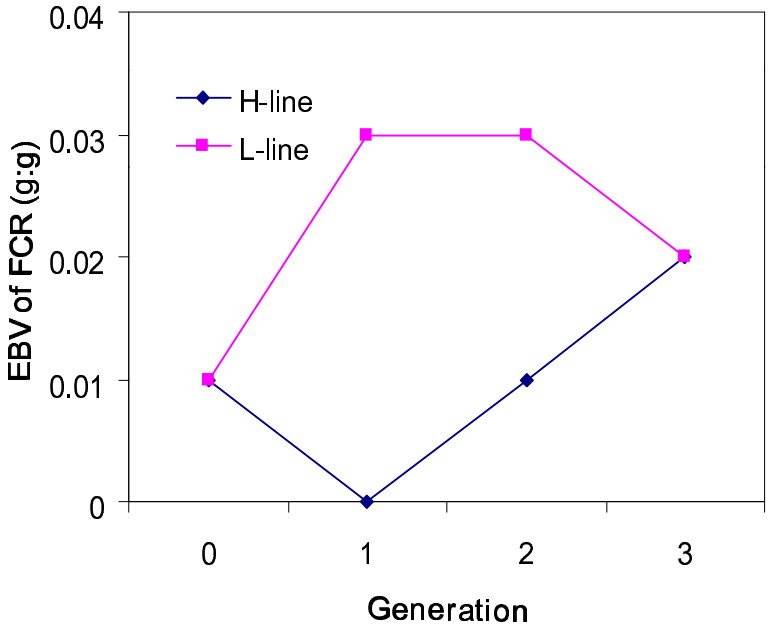

Figure 5.8 Genetic trends of feed conversion ratio (FCR) in the divergently selected lines for high or low phytate P bioavailability (PBA).

CHAPTER 6

SUMMARY

An experiment was initiated to determine genetic parameters for PBA and the genetic correlation with growth and feed utilization traits. A 3-generation divergent selection experiment was also undertaken to ascertain the efficacy of genetically improving phytate phosphorus utilization in poultry. Pedigreed data from 901 Athens-Canadian Randombred (ACRB) chickens hatched from 26 sires, 71 dams and 105 grandparents were used for the estimation of genetic parameters. Phytate P bioavailability (PBA) was estimated from the disappearance of phytate during the passage of feed through the gastrointestinal tract. Animal models, restricted maximum likelihood (REML) procedure, and the average information matrix algorithm were used for the estimation of variance components. The heritability estimate for PBA was 0.07 ± 0.02 - 0.09 ± 0.03. Genetic correlations between PBA and body weight (BW), BW gain (BWG), and feed consumption (FC) were moderate and negative, indicating that improving PBA utilization would moderately affect growth adversely.

Divergent selection for PBA demonstrated a small but significant response. At generation 3, the cumulated selection response (Rc) reached 2.56% ($P<0.01$), where Rc was calculated as the line difference in PBA after adjusting for hatch and sex effects. Best linear unbiased prediction (BLUP) selection was a time more efficient than individual phenotypic selection. Due to the influence of environmental factors, the means of phenotypic values of PBA in each line exhibited erratic fluctuations across generations. The least-square analysis based on line comparisons detected the divergent selection response but did not indicated the true genetic changes that had occurred in each line in the short-term selection project. The application of mixed model methodology with an animal model was demonstrated to be valid in the separation of observed change into its environmental and genetic components. However, the prediction of genetic trends from BLUP estimated breeding value (EBV) was still limited in accuracy. The

estimation of genetic variance using different pooled data sets demonstrated that it was not subject to selection.

The cumulated divergent correlated response (DCR_C) was evaluated for BW, BWG, FC, and FCR. The results showed a consistent correlated response in BW across generations. The DCR_C at generation 3 (G_3) was 26.8 g ($P<0.01$). The chickens in the low PBA line (L-line) had higher BW than the high PBA line (H-line). The DCR_C in BWG, FC and FCR was significant ($P<0.05$) only at G_3. The correlated responses were also evaluated with BLUP EBV. The results showed asymmetric genetic trends in BW, BWG, and FC, and the correlated responses were mainly due to the genetic changes that occurred in H-line, and little genetic change occurred in L-line across generations. FCR did not show any genetic trend. At G_3, the line differences of EBV were close to the DCR_C values for all the traits except FCR. This suggested that DCR_C and EBV criteria would tend to be consistent with the increase of generations. However, at G_1 and G_2, the line differences of the EBV actually deviated from the DCR_C values for BWG and FC. The genetic correlations of PBA with BW, BWG and FCR that were observed in the base population (G_0) became much weaker when the information of the selected generations (G_1 - G_3) was combined into the data of G_0 for the estimation, and the genetic correlations were different for the divergent lines. The mechanism still waits investigation.

The utilization efficiency of phytate P in chickens is affected by dietary level of Ca, inorganic P and Vitamin D_3. In this study, a diet containing a sub-optimal level of P was fed. Before any breeding strategy is devised, it would be worthwhile to undertake a further study with a diet acceptable for commercial production.

The disappearance of phytate during the passage of feed through the total tract was considered as the indicator of phytate P utilization in this study. Hydrolysis of phytate P may not

necessarily mean absorption, therefore the measurement may not be accurate. Before any breeding strategies involving PBA be initiated, further experiments need to be conducted with the duration for determining PBA extended beyond 3 days. In addition, to assess the selection progress adequately, the selection program should be undertaken for more generations. Meanwhile, body composition and reproductive capacity have to be evaluated.