Effects of maternal and dietary vitamin A on growth performance, meat quality, antioxidant status, and immune function of offspring broilers

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ABSTRACT The aim of this study was to evaluate the effects of maternal and dietary vitamin A (**VA**) level on growth performance, meat quality, antioxidant status, and immune function of offspring broilers. Chinese yellow-feathered breeder hens were fed a basal diet supplemented with 0, 5,400, 10,800, and 21,600 IU/kg VA for 8 wk, with 6 replicates of 22 hens per replicate. Then the offspring hatched from each of the 4 maternal groups were fed a basal diet supplemented with 0 or 5,000 IU/kg VA for 63 D. Overall, there were 8 treatment combinations, each with 6 replicate pens of 20 birds. Results showed that (1) providing VA in offspring diets increased final body weight (**FW**), average daily gain, and average daily feed intake but reduced feed-to-gain ratio and mortality of offspring broilers ($P < 0.05$), whereas maternal provision of VA did not significantly affect the growth performance and mortality of offspring broilers. Maternal or offspring VA did not affect proportion of breast or thigh muscle ($P > 0.05$). (2) Maternal feeding with 21,600 IU/kg VA increased ($P < 0.05$) pH 24 h postmortem of breast muscle, compared with those without maternal supplication of VA. Dietary provision of 5,000 IU/kg VA in the posthatching diet decreased ($P < 0.05$) drip loss, yellowness (b*) value and lightness (L*) value, and increased shear force and pH of breast muscle compared with those without dietary VA supplication. (3) Maternal or offspring VA did not affect the activities of total superoxide dismutase and glutathione peroxidase (**GSH-Px**) or the content of malondialdehyde; however, there was a significant interaction ($P < 0.05$) between maternal and offspring VA on the activity of GSH-Px in serum. (4) Dietary provision of 5,000 IU/kg VA increased ($P < 0.05$) the weight proportion of liver and bursa of fabricius, whereas maternal feeding with 21,600 IU/kg VA increased the hatchling BW. Maternal feeding with 5,400 and 21,600 IU/kg VA decreased ($P < 0.05$) splenic interferon-γ (*IFN-γ*) transcripts and increased ($P < 0.05$) those of interleukin-2 (*IL-2*) in the progeny. There were interactions ($P < 0.05$) between maternal and offspring VA on splenic *IL-2*, *IL-1β*, and *IFN-γ* expression. In summary, maternal and offspring provision of VA both had influence on meat quality and immune function in progeny broilers. Dietary VA increased growth performance, whereas the maternal VA affected the initial body weight of progeny when hatched, but the difference in performance caused by maternal VA level was able to be eliminated by dietary VA supplementation. Therefore, offspring provision had greater importance than maternal VA in the production; however, both should be considered in broiler nutrition to achieve good meat quality and immune status of broilers.

Key words: average daily gain, broiler breeder hens, cytokines, offspring broilers, vitamin A

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INTRODUCTION

As essential micronutrients, vitamins play important roles in the production of broilers, affecting egg hatching and survival of chicks, then influencing the growth and development of broilers for their entire life (Kenny and

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Kemp, 2005). Different combinations of maternal vitamins have significant effects on growth performance, immune function, and calcium and phosphorus content in tibia of offspring broilers (Peng, 2011). Maternal vitamin E supplementation affected the antioxidant capability and oxidative status of hatchling chicks (Lin et al., 2005). It is found that increased content of vitamin D (Atencio et al., 2005; Driver et al., 2006), vitamin B_{12} (Patel and Mcginnis, 1977), and biotin (Brewer and Edwards, 1972) in the diets of broiler breeders improved the growth performance of offspring broilers. The above researches suggest that maternally provided vitamins play important roles in the performance of offspring broilers.

Recent research from this laboratory showed that 10,800 IU/kg maternal vitamin A (**VA**) increased insulin-like growth factor 1 receptor transcripts, follicle stimulating hormone receptor expression, and luteinizing hormone receptor and growth hormone receptor transcripts in the walls of yellow follicles thus improved laying rate, egg-to-feed ratio, and hatchling weight of offspring broilers; it also increased their hepatic concentrations of retinol and retinyl palmitate (Chen et al., 2016). Surai et al. (1998) similarly found that supplementing the hen's diet with 3∼120 mg/kg VA increased the accumulation of VA in the embryonic liver. Taken together, these results suggest that maternally provided VA clearly played important roles in their offspring broilers, but there is no clear research about whether maternal VA had influence on growth performance, meat quality and immune function of offspring broilers, and also, whether there are possible interactions between maternal and posthatch VA on those of the broiler progeny is unknown. This experiment was aimed to investigate effects of maternal and posthatch VA level on growth performance, meat quality and immune function of offspring broilers to clarify the action of VA on broilers.

MATERIALS AND METHODS

Chicken Husbandry

The experimental protocol was approved by the Animal Care Committee of the Institute of Animal Science, Guangdong Academy of Agriculture Science, Guangzhou, P. R. China, with the approval number of GAASISA-2014-022. A total of Five hundred twenty-eight 46-wk-old Chinese yellow-feathered female broiler breeders (Lingnan, an improved meat-type breed) with similar BW (3.09 ± 0.01 kg) and laying rates were used.

A 2 × 4 factorial arrangement was used to assess effects of maternal level (0, 5,400, 10,800, and 21,600 IU/kg) and posthatch level (0 and 5,000 IU/kg) of VA. The breeder hens were randomly assigned to the 4 treatments, each with 6 replicates of 22 hens per replicate. The hens were fed a VA depleted diet containing 0.426 mg/kg β-carotene, or diets supplemented with 5,400; 10,800; or 21,600 IU/kg VA acetate (containing 5,209; 10,726; or 21,583 IU/kg VA by analysis) (provided by DSM, NL) for 8 wks. All breeders were housed in laying cages with 2 hens per cage, received 120 g of feed per bird per day and had access to fresh water *ad libitum*. Breeder hens received artificial insemination of 25 μL pooled semen per bird every 3 D. Fifty breeder males used received diet with 15,000 IU/kg VA. At the end of the eighth wk, eggs were collected and incubated as described (Chen et al., 2016), and the hatchling weights were recorded.

Two hundred forty hatchlings from each group were assigned to 12 pens (stocking density 0.38 m2/bird), and 6 pens were fed with nonsupplemented diets, whereas the other 6 were fed with diet containing 5,000 IU/kg VA. Overall, there were 8 treatment combinations, each with 6 replicate pens of 20 birds. Water and mashed diets were given *ad libitum* to broilers during the 3 phases (1 to 21 D, 22 to 42 D, then 43 to 63 D, typical marketing age for this strain). Daylight was eliminated and replaced with 18-h lighting from incandescent bulbs. The temperature of the room was maintained at 32 to 34°C for the first 3 D and then reduced by 2 to 3°C per wk to a final temperature of 26°C.

Experimental Diets

The basal diet was formulated according to Chinese Feeding Standard of Chicken recommendations (Ministry of Agriculture PRC, 2004). Details of ingredient composition and calculated nutrient contents of the basal diets for offspring broilers are provided in Table 1. The basal diet for broiler breeder hens (shown in Supplementary Table 1) was consistent with Chen et al. (2016), because this research was a continuation of Chen's.

Measurement of Growth Performance

Feed intake was recorded daily on a per replicate basis. Birds were weighed at the beginning (day 1) and end (day 21, day 42, and day 63) of each phase. Mortality was checked daily, and dead birds were recorded and weighed to adjust estimates of gain, intake, and feed conversion ratio, as appropriate. The final body weight (**FW**), average daily feed intake (**ADFI**), average daily gain (**ADG**), and feed/gain ratio (**F/G**) were calculated.

Analysis of Carcass Traits

At 21 D of age, 2 birds per replicate were deprived of feed overnight and weighed (live weight, **LW**) (TCS-150, METTLER TOLEDO, Changzhou, China) immediately before slaughter. The birds were electrically stunned and exsanguinated (DMJ, Ningguang Machinery Co., Ltd., Nanjing, China). The liver, spleen, thymus, and bursa of fabricius were dissected, blotted, and weighed (BP221S, Sartorius, Gottingen, Germany). Immune organs index = 100% × the immune organ weight/LW.

At 63 D of age, 2 birds per replicate were electrically stunned and exsanguinated. Two pieces of *pectoralis*

Table 1. Composition and calculated nutrient content of diets of offspring broilers (as-fed basis).

Ingredients, %	1 to 21 D	22 to 42 D	43 to 63 D
Corn	59.18	59.92	64.50
Soybean meal	33.71	33.00	28.07
Fish meal	1.00	0	0
Soybean oil	1.80	3.00	3.70
DL- Methionine	0.11	0.08	0.05
Limestone	1.27	1.19	1.13
Calcium monohydrogen phosphate	1.63	1.51	1.25
Salt	0.30	0.30	0.30
Vitamin and mineral premix[1]	1.00	1.00	1.00
Total	100.00	100.00	100.00
Nutrient contents[2]			
ME, MJ/kg	12.13	12.54	12.96
CP, %	21.00	19.00	17.00
Ca, %	1.00	0.90	0.80
Nonphytate phosphorus, %	0.45	0.40	0.35
Lysine, %	1.15	1.10	0.85
Methionine, %	0.45	0.40	0.34
Methionine + Cysteine, %	0.80	0.74	0.66

[1]Premix provided the following per kilogram of diets during 1 to 21 D of age: VD_3 3,300 IU, VE 20 IU, VK_3 6 mg, VB_1 1.8 mg, VB_2 9 mg, VB_6 3.5 mg, VB_{12} 0.01 mg, chloride 500 mg, niacin 60 mg, pantothenic acid 16 mg, folic acid 0.55 mg, biotin 0.15 mg, Fe 80 mg, Cu 8 mg, Mn 80 mg, Zn 60 mg, I 0.35 mg, Se 0.3 mg. Premix provided the following per kilogram of diets during 22 to 42 D of age: VD_3 3,300 IU, VE 20 IU, VK_3 6.0 mg, VB_1 3.0 mg, VB_2 9.0 mg, VB_6 6.0 mg, VB_{12} 0.03 mg, chloride 1,000 mg, niacin 60 mg, pantothenic acid 18 mg, folic acid 0.75 mg, biotin 0.10 mg, Fe 80 mg, Cu 12 mg, Mn 100 mg, Zn 75 mg, I 0.35 mg,Se 0.15 mg. Premix provided the following per kilogram of diets during 43 to 63 D of age: VD_3 1,000 IU,VE 20 IU,VK_3 4 mg,VB_1 1.8 mg,VB_2 8 mg,VB_6 3.5 mg,VB_{12} 0.01 mg, chloride 500 mg, niacin 44 mg, pantothenic acid 10 mg, folic acid 0.55 mg, biotin 0.15 mg, Fe 80 mg, Cu 8 mg, Mn 80 mg, Zn 60 mg, I 0.35 mg,Se 0.15 mg.

[2]Values were calculated from data provided by Feed Database in China (2012).

major and left thigh muscle (bone-free) were dissected and weighed. Live weight, breast muscle mass, and thigh muscle mass were recorded. Breast muscle ratio = 100% × muscle mass (2 pieces)/LW; thigh muscle ratio = 100% × 2 × muscle mass (left)/LW.

Blood and Tissue Sampling

Spleens were collected from the 21 D birds sampled and were snap-frozen. Blood samples from the wing vein of two 63 D birds were collected (171002, Transcendental medical machinery Co., Ltd, Xiong'an, China) and held on ice for < 1 h then centrifuged at 860 *g* for 15 min at 4°C (AVANTI 30; Beckman Coulter Inc, Brea, CA) to obtain serum which was then snap-frozen in liquid nitrogen and stored at −70°C until analysis.

Determination of Meat Quality

Carcasses were dissected, and indices of meat quality including color, shear force, drip loss, and pH were determined on breast muscle, all as described previously (Wang et al., 2019).

In brief, the pH was measured at 45 min and 24 h postmortem in the right pectoralis major muscle with a portable pH meter equipped with an insertion glass electrode (HI8424, HANA Instrument Science and Technology Co., Ltd, Beijing, China). Musculus pectoralis major was taken from the carcass, and samples were cut using a 25-mm cork borer at a right angle to the muscle fiber direction and then placed in a plastic bag filled with air and fastened to avoid evaporation, left at 4 to 6°C for 24 h, and drip loss was determined by weighing to calculated the water-holding capacity (BP221S, Sartorius). Lightness (L*), redness (a*), and yellowness (b*) was measured at 45 min and 24 h postmortem using a chroma meter (CR-410, KONICA MINOLTA, Tokyo, JP). The breast muscles refrigerated overnight at 4°C were cooked to an internal temperature of 70°C on a digital thermostat water bath (SHZ-28; Guowang Instrument Manufacturing Co., Ltd, Suzhou, China). After cooling to room temperature, segments 1 cm^2 were cut perpendicular to the fiber orientation of the muscle then 10 sections about 3 cm thick were cut parallel to the fiber orientation through the thickest portion of the cooked muscle. Shear force was determined using an Universal Mechanical Machine (Instron model 4411, Instron corp., Canton, MA).

Biochemical Determinations

The activities in plasma of total superoxide dismutase (**T-SOD**) and glutathione peroxidase (**GSH-Px**) and the content of malondialdehyde (**MDA**) were assayed using colorimetric kits (A001-1-2, A005-1-2 and A003-1-2, Nanjing Jiancheng Institute of Bioengineering, Nanjing, China) and a spectrophotometer (Biomate 5, Thermo Electron Corporation, Rochester, NY).

RT-PCR and Quantitative PCR

Total RNA was extracted from powdered frozen spleen of 21 D chicks (RNAiso plus 9109, Takara, Tokyo, Japan) and reverse-transcribed with PrimeScript II first Strand cDNA Synthesis Kit (6210A, Takara). Real-time PCR was performed with SYBR PremixExTaq II (Takara) and an ABI 7500 real-time PCR system (Applied Biosystems, Carlsbad, CA) (Satoh et al., 2010). The primers used for this experiment are provided in Supplementary Table 2. Results were normalized to the abundance of β-actin transcripts, and relative quantification was calculated using the $2^{-\Delta\Delta CT}$ method.

Statistical Analysis

Effects of treatment were examined by multivariate analysis of variance in the GLM procedure of SAS (ver. 8.02, 2001; SAS Inst. Inc., Cary, NC), including the main effects (maternal and dietary VA) and the interactive effect between them. The treatment means were compared by Duncan multiple range tests at $P < 0.05$ significance levels. The correlation coefficients were derived with the REG CORR procedure of SAS (as above).

RESULTS

Growth Performance of Broilers

As shown in Table 2, for starter phase broilers (1 to 21 D), there were significant effects ($P < 0.05$) of maternal VA on hatchling weight with 10,800 IU/kg VA significantly increasing the initial body weight, compared with all other maternal dietary levels. Supplemental VA in the posthatch diet increased FW, ADG, ADFI, and F/G ($P < 0.05$), but maternal VA level did not significantly affect these variables. There was significant interaction between maternal and posthatch VA on ADFI of the birds ($P < 0.05$).

As shown in Table 3, during the grower phase (day 22 to day 42), 5,000 IU/kg VA added to the grower diet significant increased FW, ADG, and ADFI and reduced F/G ($P < 0.05$), whereas VA in the maternal diet had a significant effect on day 21 to day 42 mortality. Mortality of broilers derived from 0 or 21,600 IU/kg maternal VA treatments was significantly less than those from 5,400 IU/kg maternal VA.

Performance during the finisher phase (day 43 to 63) is shown in Table 4. There were no effects of maternal supplementation with VA but supplementation of the finisher diet significantly increased FW, ADG, and ADFI and reduced F/G ($P < 0.05$).

For the whole 63 D growth period (Table 5), 5,000 IU/kg VA in the broiler diets significantly increased FW, ADG, and ADFI and reduced mortality and F/G ($P < 0.05$), compared with no added VA, whereas maternal VA was without effect. There were no significant interactions between maternal and posthatch VA on performance variables of the offspring broilers ($P > 0.05$).

Carcass Traits

There was no effect of maternal VA on carcass traits of 63 D broilers (Supplementary Table 3), but a trend was

Table 2. Effects of maternal and dietary VA on growth performance of offspring broilers from 1 to 21 D of age.[1]

Treatment							
Maternal VA	Dietary VA	Initial body weight D $_1$, g	$FW_{d\ 21}$, g	ADG, g	ADFI, g	F/G	Mortality, %
0	0	41.33	430.56	18.53	29.23^{c}	1.58	0.00
0	5,000	41.34	441.2	19.04	31.08^{a,b,c}	1.63	0.00
5,400	0	41.76	447.5	19.32	31.17^{a,b,c}	1.61	0.00
5,400	5,000	41.73	440.42	18.98	31.19^{a,b,c}	1.64	0.83
10,800	0	42.63	434.52	18.66	30.56^{b,c}	1.64	2.38
10,800	5,000	42.65	467.26	20.22	32.96^{a,b}	1.63	0.00
21,600	0	41.55	421.88	18.11	28.68^{c}	1.58	2.08
21,600	5,000	41.53	458.85	19.87	33.41^{a}	1.68	0.00
SEM		0.02	10.00	0.48	0.79	0.02	0.77
Main effect							
0		41.34^{d}	435.88	18.79	30.16	1.61	0.00
5,400		41.75^{b}	443.96	19.15	31.18	1.63	0.42
10,800		42.64^{a}	450.89	19.44	31.76	1.63	1.19
21,600		41.54^{c}	440.36	18.99	31.04	1.63	1.04
SEM		0.01	7.07	0.34	0.56	0.02	0.54
	0	41.82	433.61^{b}	18.66^{b}	29.91^{b}	1.60^{b}	1.12
	5,000	41.82	451.93^{a}	19.53^{a}	32.16^{a}	1.65^{a}	0.21
	SEM	0.01	5.00	0.24	0.40	0.01	0.38
Source of variation			*P*-values				
Maternal VA		<0.001	NS	NS	NS	NS	NS
Dietary VA		NS	0.013	0.013	<0.001	0.009	NS
Maternal VA × Dietary VA	NS	NS	NS	0.0423	NS	NS	

[a–d]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: ADFI, average daily feed intake; ADG, average daily gain; F/G, feed/gain ratio; FW, final body weight; NS, not statistically significant; VA, vitamin A.

[1]Values are means of 6 replicates per treatment with 20 broilers each. For the main effects, values are means of 12 replicates with 20 broilers each or 24 replicates with 20 broilers each, separately.

Table 3. Effects of maternal and broiler dietary VA on growth performance of offspring broilers from 22 to 42 D of age.[1]

Treatment						
Maternal VA	Dietary VA	$FW_{d\ 42}$, kg	ADG, g	ADFI, g	F/G	Mortality, %
0	0	1.06	30.05	82.41	2.76	3.70[b]
0	5,000	1.26	39.08	92.86	2.38	0.00[b]
5,400	0	1.05	28.57	78.45	2.76	8.33[a]
5,400	5,000	1.24	38.04	90.53	2.38	2.50[b]
10,800	0	1.11	32.14	84.65	2.67	1.19[b]
10,800	5,000	1.30	39.43	95.30	2.42	3.57[b]
21,600	0	1.06	30.25	83.75	2.80	1.04[b]
21,600	5,000	1.28	39.13	94.41	2.42	1.04[b]
SEM		0.03	1.46	2.43	0.09	1.51
Main effect						
0		1.16	34.57	89.25	2.62	1.85[b]
5,400		1.14	33.31	85.98	2.62	5.42[a]
10,800		1.20	35.79	92.33	2.62	2.38[a,b]
21,600		1.17	34.69	90.97	2.67	1.04[b]
SEM		0.02	1.03	1.72	0.06	1.07
	0	1.07[b]	30.25[b]	82.32[b]	2.75[a]	3.57
	5,000	1.27[a]	38.92[a]	93.27[a]	2.40[b]	1.78
	SEM	0.02	0.73	1.21	0.04	0.75
Source of variation			*P*-values			
Maternal VA		NS	NS	NS	NS	0.033
Dietary VA		<0.001	<0.001	<0.001	<0.001	NS
Maternal VA × Dietary VA		NS	NS	NS	NS	0.043

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: ADFI, average daily feed intake; ADG, average daily gain; F/G, feed/gain ratio; FW, final body weight; NS, not statistically significant; VA, vitamin A.

[1]Values are means of 6 replicates with 20 broilers each. For the main effects, values are means of 12 replicates with 20 broilers each or 24 replicates with 20 broilers each, separately.

Table 4. Effects of maternal and broiler dietary VA on growth performance of offspring broilers from 43 to 63 D of age.[1]

Treatment						
Maternal VA	Dietary VA	$FW_{d\ 63}$, kg	ADG, g	ADFI, g	F/G	Mortality, %
0	0	1.88	39.10	121.50	3.17	5.56
0	5,000	2.22	45.81	141.88	3.11	4.63
5,400	0	1.87	37.92	121.16	3.28	6.67
5,400	5,000	2.22	46.78	137.55	2.98	3.33
10,800	0	1.82	33.96	127.11	3.82	5.95
10,800	5,000	2.31	48.23	148.79	3.09	3.57
21,600	0	1.89	39.73	130.13	3.30	6.25
21,600	5,000	2.29	47.94	140.43	2.95	4.17
SEM		0.07	2.22	5.13	0.20	2.31
Main effect						
0		2.05	42.45	131.69	3.14	5.09
5,400		2.05	42.35	129.35	3.13	5.00
10,800		2.07	41.10	137.94	3.45	4.76
21,600		2.09	43.83	135.28	3.12	5.21
SEM		0.05	1.57	3.63	0.14	1.63
	0	1.87[b]	37.68[b]	124.97[b]	3.39[a]	6.11
	5,000	2.26[a]	47.19[a]	142.16[a]	3.03[b]	3.93
	SEM	0.03	1.11	2.57	0.10	1.15
Source of variation			*P*-values			
Maternal VA		NS	NS	NS	NS	NS
Dietary VA		<0.001	<0.001	<0.001	0.013	NS
Maternal VA × Dietary VA		NS	NS	NS	NS	NS

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: ADFI, average daily feed intake; ADG, average daily gain; F/G, feed/gain ratio; FW, final body weight; NS, not statistically significant; VA, vitamin A.

[1]Values are means of 6 replicates with 20 broilers each. For the main effects, values are means of 12 replicates with 20 broilers each or 24 replicates with 20 broilers each, separately.

Table 5. Effects of maternal and broiler dietary VA on growth performance of offspring broilers from 1 to 63 D of age.[1]

Treatment					
Maternal VA	Dietary VA	ADG, g	ADFI, g	F/G	Mortality, %
0	0	29.23	77.71	2.68	9.26
0	5,000	34.64	88.61	2.56	4.63
5,400	0	28.60	76.93	2.71	15.00
5,400	5,000	34.60	86.42	2.50	6.67
10,800	0	28.26	80.77	2.87	9.52
10,800	5,000	35.96	92.35	2.57	7.14
21,600	0	29.36	80.85	2.76	9.38
21,600	5,000	35.65	89.42	2.51	5.21
SEM		1.03	2.24	0.07	2.65
Main effect					
0		31.94	83.16	2.62	6.94
5,400		31.60	81.67	2.61	10.83
10,800		32.11	86.56	2.72	8.33
21,600		32.50	85.13	2.63	7.29
SEM		0.73	1.58	0.05	1.87
	0	28.86[b]	79.07[b]	2.75[a]	10.79[a]
	5,000	35.21[a]	89.20[a]	2.54[b]	5.91[b]
	SEM	0.52	1.12	0.04	1.32
Source of variation			*P*-values		
Maternal VA		NS	NS	NS	NS
Dietary VA		<0.0001	<0.0001	0.0002	0.0128
Maternal VA × Dietary VA		NS	NS	NS	NS

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: ADFI, average daily feed intake; ADG, average daily gain; F/G, feed/gain ratio; FW, final body weight; NS, not statistically significant; VA, vitamin A.

[1]Values are means of 6 replicates with 20 broilers each. For the main effects, values are means of 12 replicates with 20 broilers each or 24 replicates with 20 broilers each, separately.

Table 6. Effects of maternal and broiler dietary VA on meat quality of offspring broilers at 63 D of age.[1]

Treatment			pH value		L* value		A* value		B* value		
Maternal VA	Dietary VA	Shear force, N	45 min	24 h	45 min	24 h	45 min	24 h	45 min	24 h	Drip loss, %
0	0	29.87	6.02	5.52	56.21	61.12	16.06	14.16	11.67	13.75	2.13
0	5,000	40.38	6.04	5.51	54.06	57.98	15.91	14.76	11.67	11.84	1.96
5,400	0	32.12	5.99	5.54	55.37	59.66	16.05	14.65	13.19	13.63	2.08
5,400	5,000	35.83	6.16	5.50	54.37	58.36	16.41	14.74	12.89	12.86	1.85
10,800	0	32.48	5.94	5.61	55.02	60.03	16.32	14.57	11.61	13.32	2.07
10,800	5,000	35.40	6.12	5.52	53.76	57.05	16.49	15.35	12.02	12.90	2.01
21,600	0	31.46	5.96	5.63	54.99	59.56	16.05	14.97	12.91	14.27	2.09
21,600	5,000	34.09	6.11	5.55	54.41	57.91	15.9	15.04	10.92	11.55	2.05
SEM		1.97	0.06	0.03	0.60	0.70	0.33	0.36	0.65	0.58	0.08
Main effect											
0		35.12	6.03	5.51[b]	55.14	59.55	15.99	14.46	11.67	12.79	2.05
5,400		33.97	6.08	5.52[b]	54.87	59.01	16.23	14.69	13.04	13.25	1.97
10,800		33.94	6.03	5.57[a,b]	54.39	58.54	16.41	14.96	11.82	13.11	2.04
21,600		32.78	6.04	5.59[a]	54.7	58.74	15.98	15.01	11.91	12.91	2.07
SEM		1.43	0.04	0.02	0.42	0.50	0.23	0.25	0.47	0.42	0.06
	0	31.58[b]	5.98[b]	5.58[a]	55.40[a]	60.09[a]	16.12	14.59	12.38	13.73[a]	2.10[a]
	5,000	36.66[a]	6.10[a]	5.52[b]	54.16[b]	57.83[b]	16.18	14.96	11.88	12.26[b]	1.96[b]
	SEM	1.03	0.03	0.02	0.30	0.35	0.16	0.18	0.34	0.32	0.04
Source of variation						*P*-values					
Maternal VA		NS	NS	0.0458	NS	NS	NS	NS	NS	NS	NS
Dietary VA		0.002	0.004	0.018	0.005	<0.001	NS	NS	NS	0.002	0.029
Maternal VA × Dietary VA		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviation: NS, not statistically significant; VA, vitamin A.

[1]Values are means of 6 replicates per treatment with 2 samples each. For the main effects, values are means of 12 replicates with 2 samples each or 24 replicates with 2 samples each, separately.

observed that supplementing the broiler's diet with VA increased the ratio of breast (3.5%, $P = 0.0791$).

Meat Quality

The effects of maternal and broiler dietary VA on meat quality of 63 D offspring broilers are given in Table 6. The only significant effect of maternal VA was on pH at 24 h postmortem, where maternal supplementation with 21,600 IU/kg VA resulted in higher values than the 0 and 5,400 IU/kg treatments. There were numerous effects ($P < 0.05$) of supplementing broiler diets with 5,000 IU/kg VA, viz. on shear force, drip loss, pH, L* value, and b* value of breast muscle. In detail, VA in the broiler's diet significantly decreased drip loss, b* value 24 h postmortem, and L* values and increased shear force and pH 45 min postmortem.

Antioxidant Status

Supplementation of maternal or broiler diets with VA did not affect the activities of T-SOD and GSH-Px, nor the content of MDA in serum in broilers at 63 D of age (Table 7). There was an interaction between maternal and broiler VA on the serum activity of GSH-Px ($P < 0.05$), and the activity was highest when maternal VA was 10,800 IU/kg and dietary VA was 5,000 IU/kg in the meantime ($P < 0.05$).

Immune Organ Ratios

For 21 D chicks (Table 8), the maternal diets supplemented with VA significantly influenced liver ratio, and VA added to broiler diets increased ratios of both liver and bursa of fabricius ($P < 0.05$). Maternal treatment with 21,600 IU/kg VA resulted in heavier chick livers than did 5,400 and 10,800 IU/kg VA ($P < 0.05$).

Gene Expression

The relative abundance of splenic transcripts of several cytokines was determined in broilers aged 21 D (Table 9). Maternal supplementation with VA had significant effects ($P < 0.05$) on expression of interleukin-1β (***IL-1β***), tumor necrosis factor-α (***TNF-α***), and interferon-γ (***IFN-γ***) genes, but not interleukin-2 (***IL-2***); this last transcript was increased by supplementation of the starter diet with 5,000 IU/kg VA. Relative to the nonsupplemented diet, maternal treatment with 5,400 or 10,800 IU/kg VA increased expression of *IL-1β* ($P < 0.05$), the diet with 10,800 IU/kg VA increased expression of *TNF-α* ($P < 0.05$), and 21,600 IU/kg VA decreased expression of *IFN-γ* ($P < 0.05$). Furthermore, there were significant interactions between supplementing maternal and broiler diets with VA on expression of *IL-2, IL-1β,* and *INF-γ* of birds ($P < 0.05$); in details, compared with the control group (with no maternal or dietary VA), the *IL-2* expression was increased when

Table 7. Effects of maternal and broiler dietary VA on antioxidant activity of serum of offspring broilers at 63 D of age.[1]

Treatment				
Maternal VA	Dietary VA	T-SOD, U/mL	GSH-Px, U/mL	MDA, nmol/mL
0	0	112.14	1,952.02[b]	1.27
0	5,000	109.78	2,056.68[a,b]	1.12
5,400	0	116.27	2,082.11[a,b]	1.12
5,400	5,000	109.88	2,002.35[a,b]	1.09
10,800	0	121.45	1,882.81[b]	1.14
10,800	5,000	120.77	2,307.85[a]	1.01
21,600	0	112.33	2,202.41[a,b]	1.10
21,600	5,000	117.13	1,910.63[b]	1.15
SEM		4.73	106.99	0.07
Main effect				
0		110.96	2,004.35	1.19
5,400		113.07	2,042.23	1.11
10,800		121.11	2,095.33	1.08
21,600		114.73	2,056.52	1.13
SEM		3.27	77.73	0.05
	0	115.55	2,029.84	1.16
	5,000	114.39	2,069.38	1.09
	SEM	2.31	53.63	0.04
Source of variation			*P*-values	
Maternal VA		NS	NS	NS
Dietary VA		NS	NS	NS
Maternal VA × Dietary VA		NS	0.012	NS

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: GSH-Px, glutathione peroxidase; MDH, malondialdehyde; NS, not statistically significant; T-SOD, total superoxide dismutase; VA, vitamin A.

[1]Values are means of 6 replicates per treatment with 2 samples each. For the main effects, values are means of 12 replicates with 2 samples each or 24 replicates with 2 samples each, separately.

Table 8. Effects of maternal and broiler dietary VA on relative immune organ ratios of chicks at 21 D of age.[1]

Treatment		Ratio, %			
Maternal VA	Dietary VA	Thymus	Spleen	Bursa of fabricius	Liver
0	0	0.45	0.16	0.21	3.13
0	5,000	0.51	0.16	0.25	3.41
5,400	0	0.42	0.16	0.20	2.98
5,400	5,000	0.47	0.15	0.24	3.32
10,800	0	0.43	0.14	0.18	3.10
10,800	5,000	0.42	0.15	0.26	3.17
21,600	0	0.45	0.17	0.19	3.26
21,600	5,000	0.44	0.15	0.25	3.49
SEM		0.03	0.01	0.02	0.12
Main effect					
0		0.48	0.16	0.23	3.27[a,b]
5,400		0.44	0.15	0.22	3.15[b]
10,800		0.42	0.14	0.22	3.13[b]
21,600		0.45	0.15	0.21	3.36[a]
SEM		0.02	0.01	0.01	0.06
	0	0.44	0.15	0.19[b]	3.11[b]
	5,000	0.45	0.15	0.25[a]	3.33[a]
	SEM	0.01	0.005	0.01	0.04
Source of variation			*P*-values		
Maternal VA		NS	NS	NS	0.027
Dietary VA		NS	NS	<0.001	<0.001
Maternal VA × Dietary VA		NS	NS	NS	NS

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: NS, not statistically significant; VA, vitamin A.

[1]Values are means of 6 replicates per treatment with 2 broilers per replicate. For the main effects, values are means of 12 replicates with 2 broilers per replicate or 24 replicates with 2 broilers per replicate, separately.

maternal VA was 5,400 IU/kg and dietary VA was 5,000 IU/kg in the meantime ($P < 0.05$), and the *IL-1β* expression was increased when maternal VA was decreased when maternal VA was 5,400 IU/kg and dietary VA was 5,000 IU/kg in the meantime ($P < 0.05$), and the *IFN-γ* expression was decreased when maternal VA

Table 9. Effects of maternal and broiler dietary VA on gene expression in spleen of chicks at 21 D of age.[1]

Treatment					
Maternal VA	Dietary VA	*IL-2*	*IL-1β*	*TNF-α*	*IFN-γ*
0	0	0.97[b]	1.10[a,b]	1.16	1.39[a]
0	5,000	1.19[a,b]	1.10[a,b]	1.06	1.27[a,b]
5,400	0	1.00[b]	1.07[a,b]	0.90	0.99[a,b]
5,400	5,000	1.30[a]	0.73[c]	0.93	1.00[a,b]
10,800	0	1.14[a,b]	1.10[a,b]	0.97	1.31[a,b]
10,800	5,000	1.06[a,b]	1.32[a]	0.80	1.14[a,b]
21,600	0	1.22[a,b]	1.21[a,b]	0.81	0.89[b]
21,600	5,000	1.15[a,b]	0.80[b,c]	0.94	0.82[b]
SEM		0.22	0.20	0.15	0.20
Main effect					
0		1.16[b]	1.35[c]	0.98[b]	0.86[a]
5,400		1.36[a]	2.05[a]	1.04[b]	0.63[b]
10,800		1.28[a,b]	1.71[b]	1.17[a]	0.85[a]
21,600		1.23[a,b]	1.79[a,b]	1.04[b]	0.65[b]
SEM		0.06	0.13	0.04	0.05
	0	1.02[b]	1.69	1.07	0.79
	5,000	1.50[a]	1.75	1.05	0.73
	SEM	0.04	0.10	0.03	0.04
Source of variation			*P*-values		
Maternal VA		NS	<0.001	0.006	0.005
Dietary VA		0.001	NS	NS	NS
Maternal VA × Dietary VA		0.035	<0.001	NS	0.049

[a,b]Means with common letters within a main effect do not differ significantly ($P < 0.05$).

Abbreviations: *IL-2,* Interleukin-2; *IL-1β,* Interleukin-1β; *IFN-γ*, Interferon-γ; NS, not statistically significant; *TNF-α,* tumor necrosis factor-α; VA, vitamin A.

[1]Values are means of 6 replicates per treatment with 2 samples each. For the main effects, values are means of 12 replicates with 2 samples each or 24 replicates with 2 samples each, separately.

was 21,600 IU/kg and dietary VA was 0 or 5,000 IU/kg in the meantime ($P < 0.05$).

DISCUSSION

Effects of Supplementing Maternal and Broiler Diets With VA on Broiler Performance

Vitamin A plays an important role in the stabilization of the tissue environment, cell proliferation and differentiation, and animal embryonic development (Sporn et al., 1996; Tanumihardjo et al., 2004). It is evident from the result of the present study that 5,000 IU/kg VA in diet at all growing phases increased FW, ADG, and ADFI but reduced F/G and mortality of broilers, compared with the nonsupplemented diets. However, maternal supplementation of VA did not affect growth performance of offspring broilers, except for hatchling weight. These findings were similar to a previous study (Peng, 2011), which showed that the vitamin premix added to the broiler diet, but not maternal diets, improved growth performance of broilers. Mortality of offspring broilers mainly was slight (0.21 to 1.12%) in the starter phase but higher during grower and finisher phases and overall (<10.8 and 6% for nonsupplemented and supplemented diets). It can be speculated that the maternally derived VA stored in the liver of hatchling chickens partly satisfied the early growth need. Previous studies showed VA provided to laying broiler breeders linearly increased yolk and hepatic contents of VA (Yuan et al., 2014), and the embryonic and hatchling hepatic contents of VA were greatly increased by high levels of maternal VA provision (Surai et al., 1998).

Carcass traits are important in evaluating animal productive performance, but little is known of possible effects of dietary VA on such traits in broilers. The present results showing minimal effects of either maternal or broiler VA on the relative mass of breast or thigh muscle was similar to those of Han (Han et al., 2018).

Effects of Maternal and Broiler VA Supplementation on Meat Quality of Broilers

Meat color is an important indicator of meat quality. The present study found that 5,000 IU/kg VA in the broiler diets decreased b* value 24 h postmortem and L* value 45 min and 24 h postmortem. Hong et al. (2013) found that appropriate dietary levels (3,208∼6208 IU/kg) of VA decreased L* value and increased a* value of breast muscle of broilers, and addition of 10,000 IU/kg VA and 10 mg/kg VE also decreased L* value and increased a* value (Li et al., 2006). All findings suggest that dietary VA improved meat color. The lactic acid content in muscle after slaughter is reflected in pH, and acidity leads to denaturation of muscle protein, decrease of water retention, and whitening so as to damage meat quality (Castellini et al., 2002; Hur et al., 2009). Supplementing broiler diets with 5,000 IU/kg VA significantly decreased pH 45 min postmortem, consistent with the earlier work of Hong et al. (2013) who used 6,000 IU/kg. Water-holding capacity affects tenderness, color, and juiciness of meat, and it has been demonstrated that VA protected the integrity of cell membrane structure, prevented exudation, and thus improved muscle water holding capacity (Mikkelsen et al., 1999; Hong et al., 2013), which is consistent with the decreased drip loss in the present study.

Lower shear force and better meat quality generally reflect thinner muscle fibers and higher moisture content of the muscle (Wang et al., 2007; Hong et al., 2013). In the present experiment, however, VA added to the broiler diets increased shear force. It was worth noting that the breast muscle of nonsupplemented broilers was extremely loose and soft and had higher drip loss. Quite obviously, shear force alone is not an adequate indicator of meat quality, and it was necessary to establish an appropriate tenderness range as a criterion for evaluating meat quality.

There is no related study of potential effects of maternal supplementation with VA on meat quality of offspring broilers. Maternal VA was shown here to affect pH at 24 h postmortem, with highest values in broilers from breeders fed 10,800 and 21,600 IU/kg VA. The results indicate that VA supplementation of the breeder diet was minimally effective in influencing these indices of meat quality.

Effects of VA in Maternal and Broiler Diets on Antioxidant Status of Broilers

Vitamin A and carotenoids improve the activity of antioxidant enzymes and maintain balance between oxidation and reduction (Palace et al., 1999). Hong et al. (2013) found that adding 3,000 IU/kg VA to the diet increased total antioxidant capacity, activities of T-SOD, GSH-Px, and CAT and decreased MDA content in serum of yellow feather broilers aged 43 to 63 D. Gao et al. (2013) found that maternal lutein increased glutathione:oxidised glutathione ratio and activity of GSH-Px in liver of chickens in the first wk after hatching; thereafter, maternally derived lutein decreased and dietary lutein began to play a role. In the present experiment, maternal or broiler dietary VA did not affect the plasma activities of T-SOD and GSH-Px, nor content of MDA in offspring broilers aged 63 D, and an interaction existed between maternal and dietary VA on GSH-Px activity in serum; the activity of GSH-Px was highest when maternal VA was 10,800 IU/kg and dietary VA was 5,000 IU/kg in the meantime, that indicated that regulation of antioxidant capacity of offspring broilers should be considered both in maternal and dietary nutrients. In the present investigation, taken antioxidant status into consideration, the recommended level of maternal and dietary VA for broilers was 10,800 and 5,000 IU/kg.

Effects of Maternal and Broiler Dietary VA on Immune Function of Broilers

The immune organ ratio is an indicator of the immune status of poultry. In the present study, VA in the starter diet (5,000 IU/kg) increased the ratio of liver and bursa of fabricius, whereas maternal VA affected liver ratios in 21 D broilers. The bursal response to providing VA (∼31%) in the starter diet indicates the particular importance of dietary VA in determining development of this immune organ. Yan et al. (2014) showed that 6,000 IU/kg VA increased liver and bursa ratios, and spleen ratio decreased linearly as dietary VA increased. Li et al. (2008) found that thymus ratio decreased with increased dietary VA and VE, but the ratio of spleen or bursa of fabricius were unaffected.

Several studies (Cassani et al., 2012; Yuan et al., 2014) have confirmed that animals lacking VA have impaired immune function and reduced resistance to infection and that VA maintained health by regulating cellular immunity, humoral immunity, and nonspecific immune responses. It was found here that maternal VA affected day-21 splenic expression of *IL-1β*, *TNF-α*, and *IFN-γ* genes, and moderate maternal administration with VA increased expression of *IL-2*, *IL-1β*, and *TNF-α*, whereas VA in the starter diet increased relative expression of *IL-2*. Th1-associated cytokines including *IL-2*, *IL-1*, and *TNF-α*, which have potent T-cell growth factor activity, including the replication, maturation, and differentiation of lymphocytes and is widely considered to be key cytokines in T-cell–dependent immune responses (Malek and Bayer, 2004; Malek and Castro, 2010). These findings indicate the greater importance of maternally derived VA in promoting immune function in young, starter-phase, broilers. It was further found that 5,400 and 21,600 IU/kg maternal VA decreased expression of *IFN-γ* compared with broilers from nonsupplemented breeder hens, perhaps because the broilers with adequate VA tended to develop a Th2 immune response, rather than a Th1 immune response and secreted more INF-γ (Lessard et al., 1997). Previous study showed that B cell proliferation was reduced by retinoic acid in human cells (Chen and Ross, 2005). Because IFN-γ in relatively small amounts limited Th2 cell growth and interfered with the B cell stimulatory functions of Th2 cell cytokines (Cantorna et al., 1996), did maternal and dietary VA affect the differentiation of B lymphocyte through regulation of IFN-γ in broiler? More research is needed. Furthermore, there were significant interactions between supplementing maternal and broiler diets with VA on expression of *IL-2, IL-1β,* and *INF-γ* of offspring broilers; in details, compared with the control group (with no maternal or dietary VA), the splenic gene expression of cytokines was affected when both maternal and dietary VA were supplied. Dietary VA promoted immune function, and maternal VA also could be transferred through embryo to offspring broilers to play a role; moreover, the effects of these 2 factors were also influenced by each other, suggesting that more efforts should be made to explore the optimal maternal and dietary supplementation of VA.

CONCLUSION

Both maternal and offspring provision of VA had influence on meat quality and immune function in progeny broilers. Dietary VA supplementation increased growth performance, whereas the maternal VA affected the initial body weight of progeny when hatched, but the difference in performance caused by maternal VA level was able to be eliminated by dietary VA supplementation. Therefore, offspring provision had greater importance than maternal VA in the production; however, both should be considered in broiler nutrition to achieve good meat quality and immune status of broilers.

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SUPPLEMENTARY DATA

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