

Maternal dietary methionine supplementation influences egg production and the growth performance and meat quality of the offspring

Ranran Liu,^{*,†,1} Xiaodong Tan,^{*,†,1} Guiping Zhao,^{*,†} Ying Chen,^{*,†} Dongqin Zhao,^{*,†} Wei Li,^{*,†} Maiqing Zheng,^{*,†} and Jie Wen^{*,†,2}

^{*}*Institute of Animal Sciences, Chinese Academy of Agricultural Sciences, Beijing 100193, China; and* [†]*State Key Laboratory of Animal Nutrition, Beijing 100193, China*

ABSTRACT This study aimed to investigate the effects of maternal dietary coated methionine (**Met**) on egg production and the quality, growth performance, carcass traits, and meat quality of the offspring. In total, 288 female Ross parental chickens were randomly assigned to 3 groups with 3 replicates of 32 chickens each. From week 37 to 46, the hens of different groups were fed diets containing low (0.27% Met), adequate (0.27% Met + 0.1% coated Met) (**AM**), and high (0.27% Met + 0.2% coated Met) (**HM**) Met. There was a positive response in laying rate and albumen weight in AM and HM groups. For the offspring at market age, BW, eviscerated weight, and muscle weight were increased in the AM group ($P < 0.05$), whereas excessive supplementation was proven to be negative with those traits. The meat quality (color, pH, and shear force) of breast muscle was significantly influenced by different supplementation levels. The lightness and yellowness were increased in the HM group ($P < 0.05$, $P < 0.01$, respectively), and

redness was decreased in the AM group ($P < 0.05$). A lower pH value occurred in chickens of the HM group ($P < 0.05$). The expressions of meat quality-related genes were altered in the supplementation groups. The pH-related genes *PRDX4* and *PRKAG2* were found to be significantly differentially expressed ($P < 0.05$, $P < 0.01$, respectively) and consistent with pH changes. The meat color-related gene *BCO1* was also differentially expressed ($P < 0.01$) and showed a corresponding change with yellowness value. Collectively, the best production performance was in the offspring with 0.1% coated Met supplementation (AM group). Supplementation with 0.2% coated Met (HM group) seemed to be excessive, but laying rate was increased in the HM group. Both results of phenotypic measurements and gene expression demonstrated that maternal-coated Met supplementation resulted in fluctuation of some meat quality indices in the offspring, but all values were still within the range found in normal chickens.

Key words: coated methionine, productive trait, offspring, meat quality, gene expression

2020 Poultry Science 99:3550–3556

<https://doi.org/10.1016/j.psj.2020.03.043>

INTRODUCTION

In the early stages, the growth and development of birds depends entirely on the nutrients in eggs (Kenny and Kemp, 2005); therefore, the maternal nutrition of laying hens has a profound influence on growth and development, disease resistance, and meat quality of the offspring (Cetin et al., 2004; Zhang et al., 2014; Fan et al., 2018). As the first limiting amino acid for

chickens, the effect of maternal dietary methionine (**Met**) supplementation on hens and offsprings is largely unknown.

Previous reports have indicated that dietary Met supplementation in chickens could increase egg production and improve growth performance (Xiao et al., 2017; Zhang et al., 2017). A maternal low-protein diet has been shown to have a negative effect on egg production and on the initial BW of the offspring (Rao et al., 2009). It has also been reported that many nutrients, including energy (Zhang et al., 2018), minerals (Gao et al., 2014), vitamins (Nockels, 1979), and even toxins (Guerrero-Bosagna and Skinner, 2012), can have a trans-generational effect on offspring performance. However, the trans-generational effect of coated Met on chicken fed corn–soybean meal diets has been rarely reported.

© 2020 Published by Elsevier Inc. on behalf of Poultry Science Association Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Received October 31, 2019.

Accepted March 27, 2020.

¹Authors contributed equally.

²Corresponding author: wenjje@caas.cn

In the past decades, many studies have proven that the levels of dietary Met were closely related to egg production and egg quality, such as egg weight and albumen quality (Shafer et al., 1996, 1998). It has also been reported that dietary Met affected the growth and development of chickens (Wen et al., 2017a) and could elevate their growth performance and carcass traits (Wen et al., 2014; Hayat et al., 2015; Wen et al., 2017b; Zhang et al., 2017). However, Xue et al. (2018) reported that excessive dietary Met had a negative effect on growth performance in ducks, which was also observed in broilers (Dilger et al., 2007). For meat quality traits, Chen et al. (2013) and Conde-Aguilera et al. (2016) reported that dietary Met concentrations affected meat quality, such as pH and meat color in fast-growing chickens. However, it remains unclear whether the effects of dietary Met supplementation could be transmitted to the next generation. In pigs, maternal dietary Met supplementation was proven to affect growth performance and meat quality in offsprings (Zhuo et al., 2018).

Coated Met, a type of new Met source, has been used widely in animal production, especially in ruminant and aquatic production, owing to its protective effects and high absorption rate (Smith and Boling, 1984; Alam et al., 2005). Xiao et al. (2017) recently showed that dietary coated Met led to higher egg production and quality in chickens. Therefore, it is logical to conclude that maternal dietary coated Met supplementation will have an influence on growth performance and the carcass and meat quality traits of the offspring. In this study, we aimed to investigate the transgenerational effects of maternal supplementation of coated Met on egg production and quality, as well as on the growth performance and meat quality of the offspring.

MATERIALS AND METHODS

Animals and Experimental Diets

All procedures were approved by the Science Research Department of the Institute of Animal Sciences, CAAS (Beijing, China). A total of 288 female Ross parental chickens at the age of 36 wk (Hebei Feilong Poultry Breeding Co., Ltd., Xingtai, China) were randomly divided into 3 groups with 3 replicates, and 32 chickens for each replicate. Each group was treated with diets of different Met levels. Diets were formulated in accordance with the NRC (1994) to contain low (**LM**) (0.27% Met), adequate (**AM**) (0.37% Met), and high (**HM**) (0.47% Met) Met. The LM diets contained no supplemental Met, whereas the AM and HM diets were formulated by adding 0.1% and 0.2% coated Met in the LM diet, respectively (Table 1). Coated Met, containing 50% of active substance, was purchased from Hangzhou King Technology Feed Co., Ltd. (Hangzhou, China). Chickens were reared on the floor, and the experimental diets and water were available ad libitum for 10 wk. Thirty-two female and 4 male chickens were reared in the same pen, and

Table 1. Ingredient and nutrient composition of experimental diets (air-dry basis).

Item	LM	AM	HM
Ingredient (%)			
Corn	68.46	68.46	68.46
Soybean meal, 44% CP	22.5	22.5	22.5
Fermented soybean meal, 53.5% CP	3	2.9	2.8
Soybean oil	2	2	2
Lecithin	1.5	1.5	1.5
Dicalcium phosphate	1.24	1.24	1.24
Salt	0.3	0.3	0.3
Coated methionine	0	0.1	0.2
Premix ¹	1	1	1
Calculated composition (%) ²			
ME (Mcal/kg)	2.78	2.78	2.78
CP	16.7	16.7	16.7
Calcium	3.22	3.22	3.22
Total phosphorus	0.6	0.6	0.6
Methionine	0.27	0.37	0.47

Abbreviations: AM, adequate-Met (0.27% Met + 0.1% coated Met) group; HM, high-Met (0.27% Met + 0.2% coated Met) group; LM, low Met (0.27% Met) group.

¹The premix provided the following per kg of the diet vitamin A, 10,400 IU; vitamin D3, 2,500 IU; vitamin E, 30 IU; vitamin K3, 2 mg; vitamin B1, 2 mg; vitamin B2, 8.5 mg; vitamin B6, 4 mg; vitamin B12, 0.015 mg; folic acid, 3 mg; biotin, 2 mg; niacin, 35 mg; calcium pantothenate, 40 mg; choline chloride 400 mg; Cu, 8 mg; Fe, 80 mg; Zn, 65 mg; Mn, 80 mg; I, 1 mg; and Se, 0.3 mg.

²Nutritive values were calculated based on data provided by Chinese Feed Database in China.

offsprings were generated through random mating. The offspring chickens were reared in stair-step caging under continuous lighting using standard temperature, humidity, and ventilation conditions.

Egg Production and Quality Traits

During the experimental period, the previous 3 wk (37–39 wk) were designed as backgrounding. In the following 7 wk (40–46 wk), the egg production and egg weight were recorded every day to calculate the laying rate, and 48 eggs from each group were chosen to detect the egg quality. The yolk, albumen, and eggshell were weighed, and the eggshell strength was measured by using an Eggshell Strength Tester (EFR-01, Orka Food Technology Ltd., Ramat Hasharon, Israel). The eggshell thickness was measured by using an Eggshell Thickness Gauge (ESTG-1, Orka Food Technology Ltd., Ramat Hasharon, Israel) at 3 positions (the equator, blunt end, and sharp end) (Li et al., 2018). The albumen height, yolk color, and Haugh unit were measured by using an Egg Analyzer (EA-01, Orka Food Technology Ltd., Ramat Hasharon, Israel).

Sample Collection and Carcass Traits Determination

The offspring birds were weighed at day 1, 14, and 21. At 49 D, the offspring birds were weighed, stunned, and euthanized using approved procedures. The breast and thigh muscles and abdominal fat were stripped completely and weighed. Part of the breast and thigh

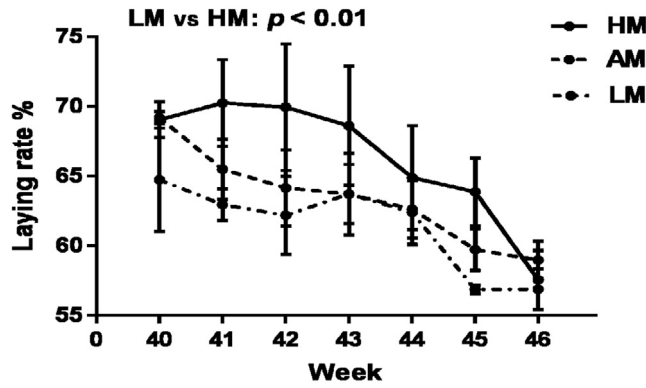


Figure 1. Effect of coated Met supplementation on laying rate. Data are presented as mean \pm SEM of 3 replicates, with 32 hens per replicate. The laying rate of the HM group was significantly higher than that of the LM group ($P < 0.01$). Abbreviations: AM, adequate-Met (0.27% Met + 0.1% coated Met) group; HM, high-Met (0.27% Met + 0.2% coated Met) group; LM, low-Met (0.27% Met) group.

muscles were collected and snap-frozen immediately in liquid nitrogen and stored at -80°C for following assay.

Determination of Meat Quality Traits

At 45 min and 24 h after slaughter, meat color ($L^*_{45 \text{ min}}$, $L^*_{24 \text{ h}}$, $a^*_{45 \text{ min}}$, $a^*_{24 \text{ h}}$, $b^*_{45 \text{ min}}$, and $b^*_{24 \text{ h}}$) of breast muscle was estimated using the CIELAB system (Gomez-Polo et al., 2017); the pH value of breast muscle was detected using a pH meter (HI8424, Hanna Instruments, Italy) (Sun et al., 2013), and the drip loss of samples was measured (Yang et al., 2016). Two grams of muscle samples were collected, and the initial weight was recorded; then, the samples were hung in a plastic bag, sealed, stored at 4°C for 24 h, and weighed. The drip loss was calculated as $(\text{weight}_{\text{initial}} - \text{weight}_{24\text{h}}) / \text{weight}_{\text{initial}} \times 100\%$. The shear force of the breast muscle and thigh muscle was measured (Devatkal et al., 2018) using a Texture Analyzer (TA.XTPlus; Stable Micro System, England).

Quantitative Real-Time PCR

The process of isolation, quantification, and reverse transcription of total RNA from breast muscle was performed as previously described (Zhang et al., 2018). The primers were designed based on chickens' coding region sequence from Ensembl database, which are shown in Table 2. The *RPL32* and *HSP70* were used to normalize the results. The quantitative real-time PCR was conducted in triplicate with the QuantStudio 7 Flex Real-Time PCR System (Applied Biosystems, MA), and the amplification protocol was as follows: 95°C for 3 min, followed by 40 cycles of 95°C for 3 s and annealing temperature for 34 s. The results were analyzed by the $2^{-\Delta\Delta\text{CT}}$ method (Livak and Schmittgen, 2001).

Statistical Analysis

The present experiment was designed based on a completely randomized design. The GLM model by one-way ANOVA was applied to analyze the data using SPSS 25 (IBM), and the Met content and the offspring's gender were considered as the fixed effect. Differences among 3 treatments were analyzed by the Bonferroni test, and significance was accepted at $P < 0.05$ or $P < 0.01$. The data given in table are presented as "mean value \pm SEM."

RESULTS

Effects of Coated Met on Egg Production and Quality in Hens

The egg production and quality results are shown in Figure 1 and Table 3. From week 40 to 46, the average laying rate of the HM group was 5% higher than that of the LM group, which was statistically significant ($P < 0.01$; Figure 1). The egg weight was significantly increased in both the AM and HM groups, and it was higher in the AM group than in the HM group ($P < 0.001$). The albumen weight was significantly elevated in the AM group, compared with the other

Table 2. Genes and primers for qRT-PCR.

Accession number	Gene	Primer	Product size (bp)
XM_015281206.2	<i>PRKAG2</i>	F:5'-TGCCTTCATACATCCAGACACTCCTAT-3' R:5'-ACCTCAGCCTTCACTATCCTATCAACA-3'	279
XM_416800.6	<i>PRDX4</i>	F:5'-CCACCCTAGCCATGGATTACC-3' R:5'-AGGCATGGCTACATCTTCGAG-3'	197
XM_015292519.2	<i>BCO1</i>	F:5'-TCCAACCTCCGCAACTGCTGTA-3' R:5'-TTGGCTCAGACACCACAACACA-3'	314
XM_004937541.2	<i>PPP1R3A</i>	F:5'-TGAACGGCATTATACGAGTCCCTCAA-3' R:5'-ATTCCACTTTGGCTCCATCTCTCTG-3'	195
XM_015293128.2	<i>RPL32</i>	F:5'-AGTTCATCCGCCACCAGTCTGAT-3' R:5'-GCTTCGTCTTCTTGTGCTCCCAT-3'	147
NM_001006685.1	<i>HSP70</i>	F:5'-TCTGCTCCTGTTGGATGTC-3' R:5'-TGGGAATGGTGGTGTACG-3'	95

Abbreviations: *BCO1*, beta-carotene oxygenase 1; F, forward; *HSP70*, heat shock 70-kDa protein 2; *PPP1R3A*, protein phosphatase 1 regulatory subunit 3A; *PRDX4*, peroxiredoxin 4; *PRKAG2*, protein kinase AMP-activated noncatalytic subunit gamma 2; qRT-PCR, quantitative real-time PCR; R, reverse; *RPL32*, ribosomal protein L32.

Table 3. Effects of coated Met supplementation on egg quality.^{1,2}

Item	LM	AM	HM	SEM	P-value
Egg weight (g)	61.97 ^C	63.06 ^A	62.44 ^B	0.134	0.000
Yolk weight (g)	20.42	20.37	20.5	0.227	0.924
Albumen weight (g)	29.71 ^B	31.36 ^A	29.52 ^B	0.451	0.008
Eggshell weight (g)	7.30	7.43	7.40	0.088	0.560
Albumen height (mm)	3.17	2.92	3.07	0.141	0.449
Yolk color	8.04	8.15	8.36	0.129	0.238
Haugh unit	43.1	39.9	43.21	2.339	0.480
Eggshell strength	4.07	4.05	4.09	0.083	0.944
Eggshell thickness (mm)	0.38	0.37	0.37	0.005	0.544

Abbreviations: AM, adequate-Met (0.27% Met + 0.1% coated Met) group; HM, high-Met (0.27% Met + 0.2% coated Met) group; LM, low-Met (0.27% Met) group.

¹Results are the mean and pooled SEM of 3 replicates per group, with at least 30 birds per replicate.

²Means within a row with no common lowercase and uppercase superscripts differ significantly at $P < 0.05$ or $P < 0.01$, respectively.

2 groups ($P < 0.01$). There were no significant differences observed among the groups for yolk and eggshell weights, albumen height, yolk color, Haugh unit, and eggshell strength and thickness ($P > 0.05$).

Effects of Coated Met on Growth Performance and Carcass Traits of Offsprings

The offspring growth performance and carcass trait results are shown in Table 4. The chickens in the AM group had higher BW at day 1 than those in the LM group ($P < 0.05$), and the chickens in the HM group had lower BW at day 49 than those in the other 2 groups ($P < 0.05$). The ADG was increased slightly in the AM group from 21 D to 49 D, though it did not reach a significant level ($P = 0.096$). Significantly higher breast muscle, thigh muscle, and eviscerated weights were observed in the AM group than in the HM group ($P < 0.01$).

Effects of Coated Met on Meat Quality of Offsprings

The meat quality results of breast muscle are shown in Table 5. Compared with that of the LM and HM groups, a lower $a^*_{45 \text{ min}}$ was observed in the AM group ($P < 0.01$); whereas a lower $a^*_{24 \text{ h}}$ was also observed compared with that of the HM group ($P < 0.05$). The chickens in the HM group had higher $L^*_{45 \text{ min}}$ than in the other 2 groups ($P < 0.01$), and the lowest $pH^*_{45 \text{ min}}$ and $pH^*_{24 \text{ h}}$ were observed in the HM group, compared with the LM or AM group ($P < 0.05$). The shear force of breast muscle was significantly decreased in the AM and HM groups ($P < 0.05$).

Effects of Coated Met on Gene Expression in Offsprings

To verify the influence of different diets on meat quality traits of offsprings, the gene expression of 4 functional genes for those traits were analyzed. A partial difference in the expression level of related genes in muscle tissue was detected (Figure 2). The transcriptional level of pH value-related gene *PPP1R3A* was downregulated in the HM group compared with the other 2 groups ($P < 0.05$ or $P < 0.01$), which positively corresponded to the alteration of pH. The genes *PRDX4* and *PRKAG2*, both related to pH value, were negatively regulated in the HM group compared with those in the LM group ($P < 0.05$) and positively correlated to pH value. The transcriptional abundance of meat color-related gene *BCO1* was negatively regulated in the HM group comparing with that of the LM group ($P < 0.05$).

DISCUSSION

This study was conducted to examine the effects of maternal coated Met level on egg production and quality, as well as the growth performance, carcass traits,

Table 4. Effects of maternal coated Met supplementation on growth performance and carcass traits.^{1,2}

Item	LM	AM	HM	SEM	P-value
BW (g)					
1 D	43.83 ^b	45.34 ^a	44.25 ^{a,b}	0.395	0.023
14 D	352.55	368.91	360.94	6.386	0.197
21 D	667.52	663.31	655.26	3.405	0.968
49 D	1920.14 ^A	2008.72 ^A	1825.85 ^B	28.093	0.000
ADG (g/d)					
1 D to 14 D	22.18	22.97	22.62	0.625	0.766
14 D to 21 D	44.74	42.39	42.04	4.255	0.900
21 D to 49 D	44.44	47.05	44.40	1.331	0.096
1 D to 49 D	38.12	39.50	36.31	0.795	0.128
Eviscerated weight (g)	1587.24 ^{a,b}	1621.07 ^a	1521.27 ^b	24.943	0.014
Breast muscle weight (g)	418.16 ^{a,b}	432.17 ^a	391.15 ^b	8.657	0.004
Thigh muscle weight (g)	463.56 ^{a,b}	473.76 ^a	447.13 ^b	7.650	0.035
Abdominal fat weight (g)	14.79	15.76	14.7	0.623	0.439

Abbreviations: AM, adequate-Met (0.27% Met + 0.1% coated Met) group; HM, high-Met (0.27% Met + 0.2% coated Met) group; LM, low-Met (0.27% Met) group.

¹Results are the mean and pooled SEM of 3 replicates per group, with at least 60 birds per replicate.

²Means within a row with no common lowercase and uppercase superscripts differ significantly at $P < 0.05$ or $P < 0.01$, respectively.

meat quality, and related gene expression of offsprings. The present study revealed that dietary supplementation of 0.2% coated Met in the HM group was correlated with a higher laying rate. The egg weight was elevated with coated Met supplementation in the AM and HM groups, but the improvement effect was better in the AM group, whereas the albumen weight was improved in the AM group. The results were consistent with previous reports, where Alagawany et al. found that dietary Met supplementation contributed to the elevation of laying rate (Alagawany et al., 2016), as well as egg weight and albumen weight in ducks and chickens (Fouad et al., 2016; Liu et al., 2017). Collectively, we concluded that Met and coated Met enhanced laying rate and egg quality, which indicated that a high maternal coated Met diet may improve performance of offsprings by raising egg quality.

Recently, some reports have emphasized that dietary Met supplementation had a positive effect on the weight gain of offspring chickens (Hayat et al., 2015; Wen et al., 2017b), but excessive Met addition might have a negative effect on weight gain. Similar trends were found in breast and thigh muscle weight gains and eviscerated weight in the present study, which closely agreed with a study by Wen et al. that found that dietary Met could improve the breast muscle weight in broilers (Wen et al., 2014). These results indicated that maternal Met supplementation contributed to increased meat production. This effect on improved growth performance was also found in pigs (Zhuo et al., 2018). Methionine is crucial to amino acid metabolism and muscle growth (Hickling et al., 1990), and the coated Met is better absorbed (Lu et al., 2014); therefore, the BW and muscle yield may be more sensitive to coated Met. In this study, it was demonstrated that adequate supplementation of coated Met (AM group) has a positive effect on growth and carcass performance, whereas excessive supplementation of coated Met (HM group) presents the negative influence on these traits.

The reports on offspring meat quality with different maternal diets remains uncomprehending. This study demonstrated that $L_{*45 \text{ min}}$ was increased in the HM group compared with that in the other 2 groups, which were basically consistent with the report by Wang et al. (Wang et al., 2009). The HM group had diminished $pH_{45 \text{ min}}$ and $pH_{24 \text{ h}}$ values compared with the LM or AM group, although all values were within the range of 5.7 to 6.1 for normal chickens (Zhang and Barbut, 2005). The shear force was reduced in the AM and HM groups compared with that of the LM group, which demonstrated that the muscle tenderness of offsprings being improved with increasing dietary Met levels. Those results indicated that a high level of maternal coated Met supplementation might result in the fluctuation of some meat quality indices (L, a, b, and pH values), but these changes were all within the normal range.

Compared with growth and carcass traits, the accuracy of meat quality (pH and meat color)

Table 5. Effects of maternal coated Met supplementation on meat quality.^{1,2}

Item	LM	AM	HM	SEM	<i>P</i> -value
$L_{*45 \text{ min}}$	47.69 ^B	47.86 ^B	48.85 ^A	0.240	0.001
$a_{*45 \text{ min}}$	2.08 ^A	1.79 ^B	2.07 ^A	0.070	0.008
$b_{*45 \text{ min}}$	3.88	3.76	4.17	0.117	0.047
$L_{*24 \text{ h}}$	55.05	55.6	55.48	0.307	0.414
$a_{*24 \text{ h}}$	2.38 ^{a,b}	2.18 ^b	2.56 ^a	0.103	0.034
$b_{*24 \text{ h}}$	6.43	6.05	6.39	0.187	0.303
$pH_{45 \text{ min}}$	6.41 ^{a,b}	6.46 ^a	6.38 ^b	0.020	0.014
$pH_{24 \text{ h}}$	5.86 ^a	5.85 ^{a,b}	5.82 ^b	0.010	0.027
Drip loss (%)	4.14	3.67	3.77	0.230	0.289
Shear force (kg)	3.66 ^a	2.98 ^b	2.99 ^b	0.180	0.013

Abbreviations: a*: redness; b*: yellowness; L*: lightness; 24 h: 24 h after slaughter; 45 min: 45 min after slaughter; AM, adequate-Met (0.27% Met + 0.1% coated Met) group; HM, high-Met (0.27% Met + 0.2% coated Met) group; LM, low-Met (0.27% Met) group.

¹Results are the mean and pooled SEM of 3 replicates per group, with at least 20 birds per replicate for drip loss and shear force, and 80 per replicate for other traits.

²Means within a row with no common lowercase and uppercase superscripts differ significantly at $P < 0.05$ or $P < 0.01$, respectively.

measurement was dependent on multiple factors, such as environmental temperature and time point control. To verify the relationship between dietary treatment and phenotypes, quantitative real-time PCR was performed on 4 genes related to meat quality. Reduced expression of *PRDX4* and *PPP1R3A* was observed in the HM group compared with that in the LM group and decreasing $pH_{24 \text{ h}}$ was detected in the HM compared with that of the LM group. The *PRDX4* gene has been reported to play a crucial role in the regulation of the pH of breast muscle in chickens and to be positively correlated with pH (Nadaf et al., 2014; Li et al., 2015). The *PPP1R3A* gene is the protein phosphatase 1 regulatory subunit, and it is essential in the glycolysis process. In addition, this study demonstrated that downregulation of the *PRKAG2* gene, which led to the falling pH value because of maternal dietary coated Met supplementation. Sibut et al. (2011) has proved elevated glycogen content was related to the diminished expression of the *PRKAG2* gene, and Przybylski et al. (1994) suggested enhanced glycogen content could result in lower pH in muscle owing to excessive glycolysis. Most of the results of this study were consistent with those of previous reports. It has been demonstrated that expression of *BCO1* is associated with differential accumulation of carotenoids (Jlali et al., 2012), and the negative relationship between gene expression and muscle yellowness has been reported (Le Bihan-Duval et al., 2011). The higher b value of 45 min was detected in the HM group than in the LM group, though the Bonferroni test did not reach significant levels ($P = 0.054$). The negative expression of *BCO1* in the HM group compared with that in the LM group was also detected, which is consistent with previous reports.

In conclusion, supplementation of maternal diet with 0.1% coated Met had a positive effect on growth performance and carcass traits of offspring. Excessive

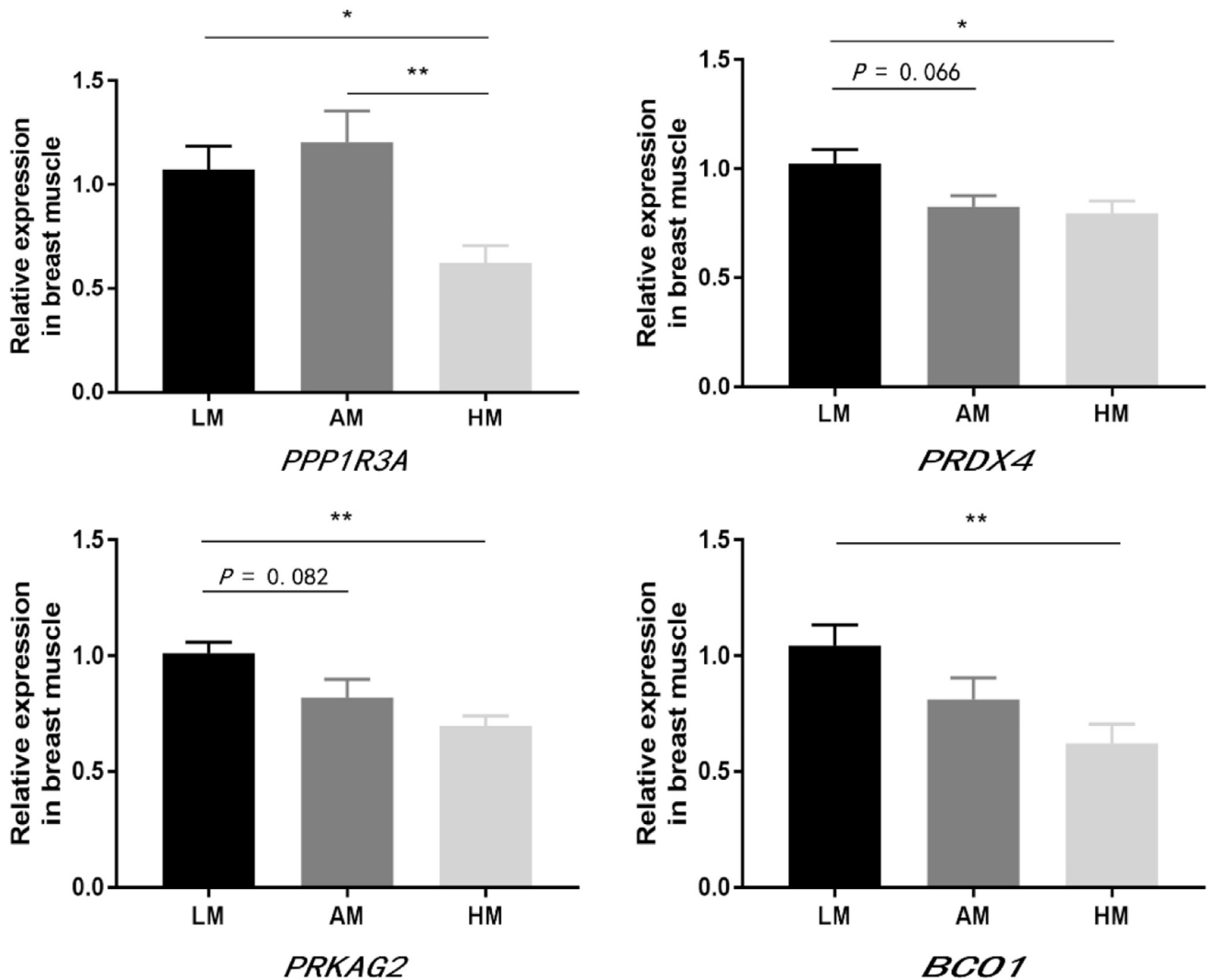


Figure 2. Relative gene expression of breast muscle of offspring with maternal coated Met supplementation. Data are presented as mean \pm SEM, $n = 12$. * represents $P < 0.05$, while ** represents $P < 0.01$. Abbreviations: AM, adequate-Met (0.27% Met + 0.1% coated Met) group; *BCO1*, beta-carotene oxygenase 1; HM, high-Met (0.27% Met + 0.2% coated Met) group; LM, low-Met (0.27% Met) group; *PPP1R3A*, protein phosphatase 1 regulatory subunit 3A; *PRDX4*, peroxiredoxin 4; *PRKAG2*, protein kinase AMP-activated noncatalytic subunit gamma 2.

supplementation of 0.2% coated Met proved to negatively impact those traits, although the laying rate was elevated significantly. Both results of phenotypic measurements and gene expression demonstrated that maternal coated Met supplementation might result in fluctuation of some meat quality indices (L, a, b, and pH values) in offsprings, but all values were still within the range of normal chickens. Furthermore, the investigation of the optimal level of coated Met in the maternal diet and the transgenerational mechanisms affected by maternal dietary Met supplementation is warranted.

ACKNOWLEDGMENTS

This study was funded by National Key Research and Development Program of China (No. 2018YFD0500401); the Modern Agro-industry Technology Research System (CARS-41) and Agricultural Science and Technology Innovation Program (ASTIP-IAS04; ASTIP-IAS-TS-15).

Conflict of Interest Statement: The authors declare no conflict of interest.

REFERENCE

- Alagawany, M., M. E. Abd El-Hack, M. Arif, and E. A. Ashour. 2016. Individual and combined effects of crude protein, methionine, and probiotic levels on laying hen productive performance and nitrogen pollution in the manure. *Environ. Sci. Pollut. Res. Int.* 23:22906–22913.
- Alam, M. S., S.-i. Teshima, S. Koshio, M. Ishikawa, O. Uyan, L. H. H. Hernandez, and F. R. Michael. 2005. Supplemental effects of coated methionine and/or lysine to soy protein isolate diet for juvenile kuruma shrimp, *Marsupenaeus japonicus*. *Aquaculture* 248:13–19.
- Cetin, I., J.-M. Foidart, M. Miozzo, T. Raun, T. Jansson, V. Tsatsaris, W. Reik, J. Cross, S. Hauguel-de-Mouzon, and N. Illsley. 2004. Fetal growth restriction: a workshop report. *Placenta* 25:753–757.
- Chen, Y. P., X. Chen, H. Zhang, and Y. M. Zhou. 2013. Effects of dietary concentrations of methionine on growth performance and oxidative status of broiler chickens with different hatching weight. *Br. Poult. Sci.* 54:531–537.
- Conde-Aguilera, J. A., J. C. Cholet, M. Lessire, Y. Mercier, S. Tesseraud, and J. van Milgen. 2016. The level and source of free-

- methionine affect body composition and breast muscle traits in growing broilers. *Poult. Sci.* 95:2322–2331.
- Devatkal, S. K., M. R. Vishnuraj, V. V. Kulkarni, and T. Kotaiah. 2018. Carcass and meat quality characterization of indigenous and improved variety of chicken genotypes. *Poult. Sci.* 97:2947–2956.
- Dilger, R. N., S. Toue, T. Kimura, R. Sakai, and D. H. Baker. 2007. Excess dietary L-cysteine, but not L-cystine, is lethal for chicks but not for rats or pigs. *J. Nutr.* 137:331–338.
- Fan, H., Z. Lv, L. Gan, and Y. Guo. 2018. Transcriptomics-related mechanisms of supplementing laying broiler Breeder hens with dietary Daidzein to improve the Immune function and growth performance of offspring. *J. Agric. Food Chem.* 66:2049–2060.
- Fouad, A. M., D. Ruan, Y. C. Lin, C. T. Zheng, H. X. Zhang, W. Chen, S. Wang, W. G. Xia, and Y. Li. 2016. Effects of dietary methionine on performance, egg quality and glutathione redox system in egg-laying ducks. *Br. Poult. Sci.* 57:818–823.
- Gao, J., Z. Lv, C. Li, Y. Yue, X. Zhao, F. Wang, and Y. Guo. 2014. Maternal zinc supplementation enhanced skeletal muscle development through increasing protein synthesis and inhibiting protein degradation of their offspring. *Biol. Trace Elem. Res.* 162:309–316.
- Gomez-Polo, C., J. Montero, M. Gomez-Polo, and A. Martin Casado. 2017. Comparison of the CIELab and CIEDE 2000 color difference Formulas on Gingival color Space. *J. Prosthodont.*
- Guerrero-Bosagna, C., and M. K. Skinner. 2012. Environmentally induced epigenetic transgenerational inheritance of phenotype and disease. *Mol. Cell. Endocrinol.* 354:3–8.
- Hayat, Z., A. U. Rehman, K. Akram, U. Farooq, and G. Saleem. 2015. Evaluation of a natural methionine source on broiler growth performance. *J. Sci. Food Agric.* 95:2462–2466.
- Hickling, D., W. Guenter, and M. Jackson. 1990. The effects of dietary methionine and lysine on broiler chicken performance and breast meat yield. *Can. J. Anim. Sci.* 70:673–678.
- Jlali, M., B. Graulet, B. Chauveau-Duriot, M. Chabault, E. Godet, S. Leroux, C. Praud, E. Le Bihan-Duval, M. J. Duclos, and C. Berri. 2012. A mutation in the promoter of the chicken beta,beta-carotene 15,15'-monooxygenase 1 gene alters xanthophyll metabolism through a selective effect on its mRNA abundance in the breast muscle. *J. Anim. Sci.* 90:4280–4288.
- Kenny, M., and C. Kemp. 2005. Breeder nutrition and chick quality. *Int. Hatchery. Pract.* 19:7–11.
- Le Bihan-Duval, E., J. Nadaf, C. Berri, F. Pitel, B. Graulet, E. Godet, S. Y. Leroux, O. Demeure, S. Lagarrigue, C. Duby, L. A. Cogburn, C. M. Beaumont, and M. J. Duclos. 2011. Detection of a Cis [corrected] eQTL controlling BCMO1 gene expression leads to the identification of a QTG for chicken breast meat color. *PLoS One.* 6:e14825.
- Li, X., X. Liu, J. Nadaf, E. Le Bihan-Duval, C. Berri, I. Dunn, R. Talbot, and D. J. De Koning. 2015. Using Targeted Resequencing for identification of candidate genes and SNPs for a QTL affecting the pH value of chicken meat. *G3 (Bethesda)* 5:2085–2089.
- Li, L. L., N. N. Zhang, Y. J. Gong, M. Y. Zhou, H. Q. Zhan, and X. T. Zou. 2018. Effects of dietary Mn-methionine supplementation on the egg quality of laying hens. *Poult. Sci.* 97:247–254.
- Liu, Y., X. Lin, X. Zhou, D. Wan, Z. Wang, X. Wu, and Y. Yin. 2017. Effects of dynamic feeding low and high methionine diets on egg quality traits in laying hens. *Poult. Sci.* 96:1459–1465.
- Livak, K. J., and T. D. Schmittgen. 2001. Analysis of relative gene expression data using real-time quantitative PCR and the 2⁻(Delta Delta C(T)) Method. *Methods* 25:402–408.
- Lu, J., Y. Hua, W.-z. Fu, F. Zhou, B.-b. Yang, J.-x. Xiao, M.-h. Liu, and Q.-j. Shao. 2014. Effects of supplementation coated lysine and methionine in mixture protein diets on growth performance, digestibility and serum biochemical indices of juvenile Black Sea bream, *Acanthopagrus Schlegelii*. *Turk. J. Fish. Aquat. Sc.* 14:633–642.
- Nadaf, J., C. Berri, I. Dunn, E. Godet, E. Le Bihan-Duval, and D. J. De Koning. 2014. An expression QTL of closely linked candidate genes affects pH of meat in chickens. *Genetics* 196:867–874.
- Nockels, C. F. 1979. Protective effects of supplemental vitamin E against infection. *Fed. Proc.* 38:2134–2138.
- Przybylski, W., P. Vermin, and G. Monin. 1994. Relationship between glycolytic potential and ultimate pH in bovine, porcine and ovine muscles. *J. Muscle Foods* 5:245–255.
- Rao, K., J. Xie, X. Yang, L. Chen, R. Grossmann, and R. Zhao. 2009. Maternal low-protein diet programmes offspring growth in association with alterations in yolk leptin deposition and gene expression in yolk-sac membrane, hypothalamus and muscle of developing Langshan chicken embryos. *Br. J. Nutr.* 102:848–857.
- Shafer, D. J., J. B. Carey, and J. F. Prochaska. 1996. Effect of dietary methionine intake on egg component yield and composition. *Poult. Sci.* 75:1080–1085.
- Shafer, D. J., J. B. Carey, J. F. Prochaska, and A. R. Sams. 1998. Dietary methionine intake effects on egg component yield, composition, functionality, and texture profile analysis. *Poult. Sci.* 77:1056–1062.
- Sibut, V., C. Hennequet-Antier, E. Le Bihan-Duval, S. Marthey, M. J. Duclos, and C. Berri. 2011. Identification of differentially expressed genes in chickens differing in muscle glycogen content and meat quality. *BMC Genomics* 12:112.
- Smith, S. I., and J. A. Boling. 1984. Lipid coating as a mode of protecting free methionine from ruminal degradation. *J. Anim. Sci.* 58:187–193.
- Sun, Y., G. Zhao, R. Liu, M. Zheng, Y. Hu, D. Wu, L. Zhang, P. Li, and J. Wen. 2013. The identification of 14 new genes for meat quality traits in chicken using a genome-wide association study. *BMC Genomics.* 14:458.
- Wang, Z. G., X. J. Pan, Z. Q. Peng, R. Q. Zhao, and G. H. Zhou. 2009. Methionine and selenium yeast supplementation of the maternal diets affects color, water-holding capacity, and oxidative stability of their male offspring meat at the early stage. *Poult. Sci.* 88:1096–1101.
- Wen, C., X. Y. Jiang, L. R. Ding, T. Wang, and Y. M. Zhou. 2017a. Effects of dietary methionine on growth performance, meat quality and oxidative status of breast muscle in fast- and slow-growing broilers. *Poult. Sci.* 96:1707–1714.
- Wen, C., X. Jiang, L. Ding, T. Wang, and Y. Zhou. 2017b. Effects of dietary methionine on breast muscle growth, myogenic gene expression and IGF-I signaling in fast- and slow-growing broilers. *Sci. Rep.* 7:1924.
- Wen, C., P. Wu, Y. Chen, T. Wang, and Y. Zhou. 2014. Methionine improves the performance and breast muscle growth of broilers with lower hatching weight by altering the expression of genes associated with the insulin-like growth factor-I signalling pathway. *Br. J. Nutr.* 111:201–206.
- Xiao, X., Y. Wang, W. Liu, T. Ju, and X. Zhan. 2017. Effects of different methionine sources on production and reproduction performance, egg quality and serum biochemical indices of broiler breeders. *Asian-australas J. Anim. Sci.* 30:828–833.
- Xue, J. J., M. Xie, J. Tang, W. Huang, Q. Zhang, and S. S. Hou. 2018. Effects of excess DL- and L-methionine on growth performance of starter Pekin ducks. *Poult. Sci.* 97:946–950.
- Yang, W. L., Y. P. Chen, Y. F. Cheng, X. H. Li, R. Q. Zhang, C. Wen, and Y. M. Zhou. 2016. An evaluation of zinc bearing palygorskite inclusion on the growth performance, mineral content, meat quality, and antioxidant status of broilers. *Poult. Sci.* 95:878–885.
- Zhang, L., and S. Barbut. 2005. Rheological characteristics of fresh and frozen PSE, normal and DFD chicken breast meat. *Br. Poult. Sci.* 46:687–693.
- Zhang, Y., Z. Liu, R. Liu, J. Wang, M. Zheng, Q. Li, H. Cui, G. Zhao, and J. Wen. 2018. Alteration of Hepatic gene expression along with the Inherited phenotype of Acquired fatty Liver in chicken. *Genes (Basel)* 9:199.
- Zhang, S., B. Saremi, E. R. Gilbert, and E. A. Wong. 2017. Physiological and biochemical aspects of methionine isomers and a methionine analogue in broilers. *Poult. Sci.* 96:425–439.
- Zhang, L., Y. X. Wang, Y. Zhou, L. Zheng, X. A. Zhan, and Q. H. Pu. 2014. Different sources of maternal selenium affect selenium retention, antioxidant status, and meat quality of 56-day-old offspring of broiler breeders. *Poult. Sci.* 93:2210–2219.
- Zhuo, Y., J. Wang, H. Liu, D. Mou, T. Adebawale, L. Che, Z. Fang, S. Xu, G. Liu, and Y. Lin. 2018. Effects of maternal methyl donor on the pork characteristics of offspring pigs with prenatal exposure to bisphenol A. *Animal* 12:1306–1315.