Effects of energy-restricted feeding during rearing on sexual maturation and reproductive performance of Rugao layer breeders

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ABSTRACT The aim of this study was to assess the effects of energy-restricted feeding during rearing on the sexual maturation and reproductive performance of Rugao layer breeders. A total of 2,400 8-wk-old Rugao layer breeders were randomly assigned to one of 5 groups (480 pullets per group) with eight replicates and were fed one of 5 diets that were nutritionally similar with the exception of apparent metabolizable energy corrected for nitrogen (**AME_n**) content (2,850, 2,750, 2,650, 2,550, and 2,450 kcal AME_n/kg) from 8 to 18 wks of age. The daily amount of feed was restricted to the absolute quantity of the diet consumed by laying hens fed 2,850 kcal AME_n per kg diet ad libitum (control). From 18 to 52 wks of age, all hens were fed basal diets ad libitum. The body weight of layer breeders at 18 wks of age decreased linearly with increasing energy restriction ($P < 0.001$), but caught up within 3 wks of ad libitum feeding ($P = 0.290$). The coefficient of variation of the body weight of the hens at 18, 21, and 24 wks of age decreased linearly ($P = 0.010$, 0.025, and 0.041, respectively) with increasing energy restriction during rearing. Energy-restricted feeding delayed sexual organ development at 18, 20, and 22 wks of age, including the number of large yellow follicles, oviduct length, oviduct length index, oviduct index, and ovary stroma index ($P < 0.05$), and delayed sexual maturity, including the age at laying the first egg and the age at 5% and 50% egg production ($P = 0.042$, 0.004, and 0.029, respectively). Consequently, egg number from 5% to 50% egg production decreased linearly as the degree of energy restriction increased ($P = 0.001$) and egg production of hens in the energy-restricted feeding groups was lower than that of hens in the ad libitum feeding group (6.36, 6.43, 6.4, and 4.61% vs. 14.29%; $P < 0.05$) from 18 to 20 wks of age. Furthermore, egg weight increased linearly as energy restriction increased ($P < 0.001$) and laying hens in the most severe energy-restricted feeding group had more setting eggs (normal eggs weighing >40 g) than hens in the ad libitum feeding and lighter energy-restricted feeding groups (149.57 vs. 144.34, 142.66, 143.63, and 141.78; $P < 0.05$). No significant differences were observed in fertility, hatchability of fertile eggs, and hatchability of setting eggs ($P = 0.381$, 0.790, and 0.605, respectively). In conclusion, moderate energy restriction (85.97%, 2,450 vs. 2,850 kcal AME_n/kg) from 8 to 18 wks of age increased egg weight as well as the production of setting eggs in native layer breeders throughout the laying period, without adverse effects on productive performance from 18 to 52 wks of age, or fertility and hatchability at 52 wks of age.

Key words: layer breeder, energy-restricted feeding, sexual organ development, sexual maturity, reproductive performance

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INTRODUCTION

China has been the world's largest poultry and poultry egg producer for more than 30 yr. According to the China Animal Agriculture Association, the egg output from laying hens was 28.13 million tons in 2019, accounting for about 40% of the world's total production, of which the eggs from certified layer breeds using local chicken resources represented about 60%. Also, the

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average stock of commercial laying hens in China was 1.05 billion in 2019, accounting for about 35% of the world's total stock, of which the certified layer breeds using local chicken resources represented about 50%. Certified layer breeds, which are popular for the unique flavor of their egg, are normally bred from local breeds. With the increase in consumption, the demand for native chickens and traditional eggs continues to grow. However, the major problem affecting the reproductive performance of crossbreeding systems is that the egg weight at the onset of the egg-laying cycle is insufficient for use as hatching eggs.

The rearing period is one of the most important stages in the life of a laying hen and the development of size, skeleton, muscle, gastrointestinal tract, and visceral and reproductive organs occurs in this phase (Bestman et al., 2012). However, relatively few studies have focused on the rearing period of laying hens to increase egg weight and production (Guzmán et al., 2016; Saldaña et al., 2016). In broiler breeders, various feeding management practices, including dietary restriction during the rearing phase, have been applied to optimize body weight (**BW**) for reproductive performance, but have resulted in potential negative effects on the length of the laying period because of the delay in sexual maturity (Leeson et al., 1997; Zuidhof et al., 2015, 2017; Hadinia et al., 2018). However, this potential disadvantage is thought to be compensated by added benefits in terms of increased production of total eggs and settable eggs, greater average egg weight, and improved fertility, hatchability, and egg quality (Hocking et al., 1989; Fattori et al., 1991; Yu et al., 1992; Hocking, 1993; Renema et al., 1999; Renema and Robinson, 2004). Hence, the feed restriction methods used for broiler breeders could be used for layer breeders to slow the growth rate of sexual organs, delay sexual maturity, increase the average egg weight, and improve the reproductive performance, particularly for hens laying small eggs at the initiation of the laying period.

The Rugao laying hen was approved as the national cultivated laying hen breed of China by the National Examination and Approval Committee of Domestic Animal and Poultry Breeds in 2009. It is typically used as the female parent of Suqin blue-eggshell chickens, which was approved as a crossbreeding system in 2013. The average BW of a Rugao laying hen is about 1.1 and 1.7 kg at 18 and 52 wks of age, respectively (Lu et al, 2017). Consequently, the Rugao laying hen can be used as a typical model of the certified crossbreeding systems with small eggs at the onset of the egg-laying cycle.

Based on the above literature, the objective of the present study was to investigate the influence of energy-restricted feeding during the rearing phase on sexual maturation and reproductive performance of Rugao layer breeders, including sexual organ development, age at laying the first egg, age at 5% and 50% egg production, laying rate curve, setting eggs number, fertility, and hatchability.

MATERIALS AND METHODS

Study Design, Birds, and Diets

A total of 2,400, 8-wk-old, Rugao layer breeders were randomly assigned to one of five groups (480 pullets per group) with 8 replicates of 60 hens each and fed one of 5 diets that were nutritionally similar with the exception of apparent metabolizable energy corrected for nitrogen (**AME_n**) content from 8 to 18 weeks of age. The calculated AME_n values were 2,850, 2,750, 2,650, 2,550, and 2,450 kcal/kg, respectively (Table 1). Feed was provided ad libitum for the laying hens at 2,850 kcal AME_n per kg diet (control). The amount of feed given to the laying hens in the other groups was restricted to the absolute quantity of the diet consumed by the hens in the control group. From 18 to 52 wks of age, all experimental laying hens were fed basal diets (Table 2) formulated to meet the National Research Council (1994) recommendations for laying hens. Water and feed were provided ad libitum. The experiment lasted from 8 to 52 wks of age,

Table 1. Ingredients and nutrient levels of the experimental diet provided from 8 to 18 wks of age.[1]

	Control	Energy-restricted feeding			
AME_n, kcal/kg	2,850	2,750	2,650	2,550	2,450
Ingredient (%)					
Corn	71.95	68.47	64.99	61.50	58.02
Soybean meal	21.80	22.17	23.03	23.65	24.27
Quartz sand	2	2	2	2	2
Limestone	1.56	1.55	1.55	1.55	1.55
Zeolite powder	0.67	3.78	6.40	9.27	12.12
Calcium hydrogen phosphate	0.87	0.88	0.88	0.88	0.89
Sodium chloride	0.35	0.35	0.35	0.35	0.35
50% Choline chloride	0.20	0.20	0.20	0.20	0.20
DL-Met	0.10	0.10	0.10	0.10	0.10
Vitamin and trace mineral premix [2]	0.50	0.50	0.50	0.50	0.50
Nutrient levels (calculated)					
AME_n (kcal/kg)	2,850	2,750	2,650	2,550	2,450
Crude protein (%)	15.50	15.50	15.50	15.50	15.50
Digestible amino acid (%)					
Lysine	0.67	0.66	0.67	0.66	0.66
Methionine	0.32	0.32	0.32	0.32	0.32
Methionine + Cystine	0.54	0.53	0.53	0.54	0.53
Arginine	0.99	0.99	1.00	1.00	1.01
Threonine	0.45	0.45	0.45	0.46	0.46
Calcium (%)	0.88	0.88	0.88	0.88	0.88
Total phosphorus (%)	0.56	0.55	0.55	0.54	0.54
Digestible phosphorus (%)	0.38	0.38	0.38	0.38	0.38
Nutrient levels (measured)					
DM (%)	92.2	91.8	93.1	92.6	92.3
Gross energy (kcal/kg)	3,977	3,812	3,769	3,603	3,562
Crude protein (%)	15.57	15.55	15.63	15.61	15.58
Total amino acid (%)					
Lysine	0.77	0.78	0.79	0.80	0.77
Methionine	0.34	0.33	0.34	0.34	0.35
Methionine + Cystine	0.65	0.65	0.65	0.65	0.65
Arginine	1.09	1.10	1.08	1.07	1.09
Threonine	0.54	0.56	0.55	0.57	0.55
Calcium (%)	0.90	0.90	0.86	0.88	0.91
Total phosphorus (%)	0.57	0.53	0.56	0.56	0.55

[1]Values are expressed on an air-dry basis.

[2]Premix includes (per kg of diet): vitamin A, 8,800 IU; vitamin D_3, 3,300 IU; vitamin E, 60 IU; cobalamin, 23 μg; riboflavin, 5.5 mg; niacin, 30 mg; pantothenic acid, 8 mg; choline, 500 mg; menadione, 1.2 mg; folic acid, 0.9 mg; pyridoxine, 1.2 mg; thiamine, 1.7 mg; biotin, 55 μg; manganese, 90 mg; zinc, 86 mg; iron, 55 mg; copper, 5.5 mg; iodine, 1.6 mg; and selenium, 0.3 mg.

Table 2. Ingredients and nutrient levels of the experimental diet provided from 18 to 52 wks of age.[1]

	18–21 wks	21–52 wks
Ingredient (%)		
Corn	66.00	65.00
Soybean meal	25.00	24.67
Wheat	1.67	-
Shell powder	3.33	6.41
Limestone	1.33	2.00
Zeolite powder	0.60	
Calcium hydrogen phosphate	1.00	0.83
Sodium chloride	0.30	0.30
50% Choline chloride	0.17	0.17
DL-Met	0.10	0.12
Vitamin and trace mineral premix [2]	0.50	0.50
Nutrient levels (calculated)		
AME_n (kcal/kg)	2,750	2,700
Crude protein (%)	17.00	16.50
Digestible amino acid (%)		
Lysine	0.73	0.72
Methionine	0.34	0.35
Methionine + Cystine	0.56	0.57
Arginine	1.08	1.05
Threonine	0.49	0.48
Calcium (%)	2.00	3.35
Total phosphorus (%)	0.60	0.57
Digestible phosphorus (%)	0.40	0.39
Nutrient levels (measured)		
DM (%)	92.7	91.6
Gross energy (kcal/kg)	3904	3841
Crude protein (%)	16.93	16.56
Total amino acid (%)		
Lysine	0.83	0.79
Methionine	0.37	0.35
Methionine + Cystine	0.67	0.61
Arginine	1.15	1.03
Threonine	0.62	0.57
Calcium (%)	1.98	3.47
Total phosphorus (%)	0.62	0.60

[1]Values are expressed on an air-dry basis.

[2]Premix includes (per kg of diet): vitamin A, 8,800 IU; vitamin D_3, 3,300 IU; vitamin E, 60 IU; cobalamin, 23 μg; riboflavin, 5.5 mg; niacin, 30 mg; pantothenic acid, 8 mg; choline, 500 mg; menadione, 1.2 mg; folic acid, 0.9 mg; pyridoxine, 1.2 mg; thiamine, 1.7 mg; biotin, 55 μg; manganese, 90 mg; zinc, 86 mg; iron, 55 mg; copper, 5.5 mg; iodine, 1.6 mg; and selenium, 0.3 mg.

which included the rearing and laying periods. The laying period lasted for 8 periods of 4 wks each (20−52 wk), with the exception of the first period, which lasted for 2 wk (18−20 wk).

Samples of diets were ground to pass through a 40-mesh sieve and immediately frozen and stored at −20°C for further analysis. The moisture contents of the diets were determined by oven-drying (930.15, AOAC, 2005). Gross energy was determined with an adiabatic bomb calorimeter (Model 1356; Parr Instrument Company, Moline, IL). Calcium content was determined by atomic absorption spectrophotometry (Beijing Beifen-Ruili Analytical Instrument (Group) Co., Ltd., Yangzhou, China; 927.02; AOAC, 2005). Phosphorus content was determined photometrically in orthophosphate from filtered ash solutions with the vanado-molybdate method (927.02; AOAC, 2005). The total nitrogen content of the samples was determined with the micro-Kjeldahl method (990.03; AOAC, 2005). Crude protein (**CP**) was calculated as nitrogen × 6.25. The amino acid content was assayed according to the method described by Wang et al. (2008) with an ion-exchange high-performance liquid chromatography system (Waters Corporation, Wilford, MA) in accordance with AOAC method 994.12 (sulfur and regular; AOAC, 2005), with postcolumn o-phthalaldehyde derivatization and fluorescence detection following acid hydrolysis. Duplicate samples of the diets (5 mg) were hydrolyzed in 1,000 μL of 6 M HCl containing 0.1% phenol for 24 h at 110 ± 2°C in vacuum-sealed glass tubes. The contents of glycine and tryptophan, which are destroyed by acid hydrolysis, were not determined.

Husbandry

This trial was carried out at the Poultry Institute of the Chinese Academy of Agricultural Sciences (Yangzhou City, Jiangsu, China) from July 2019 to May 2020. From 8 to 18 wks of age, each replicate of 60 hens was randomly assigned to 20 cages of 3 hens each. From 18 to 52 wks of age, all hens were transferred to a laying house and caged individually at a constant temperature of 24 ± 3°C and relative humidity of 65% to 75%. Light exposure was limited to 8 h from 8 to 18 wks of age and then increased by 1 h per wk until 16 h. One cage remained empty and chipboard was inserted into the feeders between the different replicate cages to prevent hens in one replicate from eating the feed of another. All animal handing protocols were approved by the Animal Care and Use Committee of the Poultry Institute. Cage-side observations, which included recording any change in clinical condition or behavior, were made at least twice per day throughout the study period.

Sample Collection and Analytical Determination

BW and Uniformity All hens were weighed individually at weekly intervals from 8 to 28 wks of age and at 52 wks of age. The coefficient of variation (**CV**) was used as an indirect measurement of BW uniformity by replicates among the laying pullets, as described by Peak et al. (2000) and Guzmán et al. (2016). The CV was calculated using the following formula:

$$CV = (\textit{standard deviation}/\text{average BW}) \times 100\%.$$

Productive Performance Daily egg number per hen was recorded individually. Daily egg weight was monitored individually until 28 wks of age, when all individual eggs weighed more than 40 g. Afterward, eggs were collected daily and the weights of all eggs laid during the last 2 days of each week were measured, individually. Eggs weighing >40 g can be used as setting eggs of native layer breeders in the Chinese layer breeder industry. Feed consumption was measured on a replicate basis at weekly intervals. From these data, egg number, egg mass, average feed consumption, feed conversion ratio (**FCR**) per kg and per dozen eggs were determined by period and cumulatively. In addition, the average daily energy and CP consumption were expressed as kcal AME and g CP consumed per day. Energy efficiency expressed as kcal AME per g of egg and CP efficiency expressed as g CP per g of egg were also calculated by period and cumulatively. Mortality was recorded when it occurred.

Sexual Organ Development Two birds from each replicate were sacrificed by direct cervical dislocation at 18, 20, 22, 24, 26, and 28 wks of age for characterization of the sexual organs. The number of large yellow follicles (greater than 10 mm in diameter) and the oviduct length were measured (Lu et al., 2019). The large yellow follicles, oviduct (emptied of contents), and ovary stroma were weighed. The index was calculated as the percentage of live BW.

Sexual Maturity Age and BW at the time of laying the first egg were recorded for each hen. Daily egg number per hen was recorded. Age at 5, 50, and 80% egg production was calculated for each replicate, and the time and egg number was calculated accordingly.

Reproductive Performance Laying rate was calculated as the total number of eggs divided by the total number of days and expressed as the average hen-day production by week and period. The following egg laying rate curve model (Yang et al., 1989) was used to fit the egg production curve:

$$y(t) = ae^{-bt}/\left[\left(1+e^{-c(t-d)}\right)\right]$$

where y_t = laying rate (%), t = age (wk), a = a scale variable, b = rate of decrease in laying ability, c = the reciprocal indicator of the variation in sexual maturity, and d = mean age of sexual maturity.

Fertility and Hatchability At 52 wks of age, the remaining hens in each group were subjected to artificial insemination and hatching eggs were collected for 6 consecutive days to calculate fertility, hatchability of fertile eggs, and hatchability of setting eggs (Lu et al., 2017). Hatching was carried out in the same incubator in accordance with the incubation program (Qingdao Xingyi Electronic Equipment Co. Ltd., Shandong, China).

Statistical Analysis

All data analyses were conducted using SPSS for Windows, version 16.0 (SPSS Inc., Chicago, IL). One-way analysis of variance followed by Duncan's multiple comparison test was used to identify differences in means among treatments. Regression curve estimation was also used to determine linear and quadratic responses of hens to different energy restrictions. Differences were reported where $P \leq 0.05$.

RESULTS AND DISCUSSION

Energy-Restricted Feeding Model

Feed and calculated AME_n consumption of energy-restricted layer breeders from 8 to 18 wks of age are presented in Table 3. Feed consumption of hens in all treatments was similar in each phase from 8 to 18 wks of age ($P = 0.920$). Calculated AME_n consumption decreased linearly from 8 to 13 ($P < 0.001$), 13 to 18 ($P < 0.001$), and 8 to 18 wks of age ($P < 0.001$) as the degree of energy restriction increased. Hence, the energy-restricted feeding model during the rearing period was established successfully. Briefly, the difference among the treatments in the energy-restricted feeding model was the difference in AME_n consumption from 8 to 18 wks of age.

BW and Uniformity

The effects of energy-restricted feeding on the BW and BW CV of layer breeders are presented in Figures 1 and 2, respectively. No statistically significant difference was observed in the initial BW and BW CV (8 wks of age; $P > 0.05$).

The BW of laying hens at 18 wks of age (after 10 wks of energy-restricted feeding) decreased linearly with increasing energy restriction (1099.44, 1073.78, 1050.67, 1021.89, and 1011.75; L, $r^2 = 0.854$, $P < 0.001$; Q, $r^2 = 0.861$, $P < 0.001$), and similar significant differences in BW were also observed after the switch to basal diets for 1 (19 wks of age; 1138.20, 1124.20, 1108.19, 1091.40, and 1085.66; L, $r^2 = 0.783$, $P < 0.001$; Q, $r^2 = 0.788$, $P < 0.001$) and 2 (20 wks of age; 1180.21, 1168.91, 1157.02, 1142.60, and 1146.92; L, $r^2 = 0.750$, $P < 0.001$; Q, $r^2 = 0.773$, $P < 0.001$) wks. No statistically significant difference was observed in BW among the groups after

Table 3. Feed consumption (g/hen per day) and AME_n consumption (kcal AME_n/hen per day) of laying pullets from 8 to 18 wks of age.[1]

	Control	Energy-restricted feeding (9–18 wks)					P value		
AME_n, kcal/kg	2,850	2,750	2,650	2,550	2,450	SEM	Energy restriction level	Linear	Quadratic
8–13 wks									
Feed consumption	43.14	43.14	43.14	43.15	43.14	0.003	0.920	0.877	0.575
AME_n consumption[2]	122.87[a]	118.64[b]	114.33[c]	110.03[d]	105.70[e]	0.973	<0.001	<0.001	0.593
13–18 wks									
Feed consumption	52.12	52.12	52.12	52.12	52.12	0.000	0.421	1.000	0.240
AME_n consumption	148.55[a]	143.33[b]	138.12[c]	132.91[d]	127.69[e]	1.180	<0.001	<0.001	0.810
8–18 wks									
Feed consumption	47.62	47.63	47.63	47.64	47.63	0.007	0.920	0.464	0.591
AME_n consumption	135.71[a]	130.99[b]	126.22[c]	121.47[d]	116.70[e]	1.076	<0.001	<0.001	0.646

[a-e]Means without common superscripts within a row differ significantly ($P < 0.05$).
[1]Values are means of eight replicates per dietary treatment.
[2]All the AME_n values of the diets are calculated, as presented in Table 1.

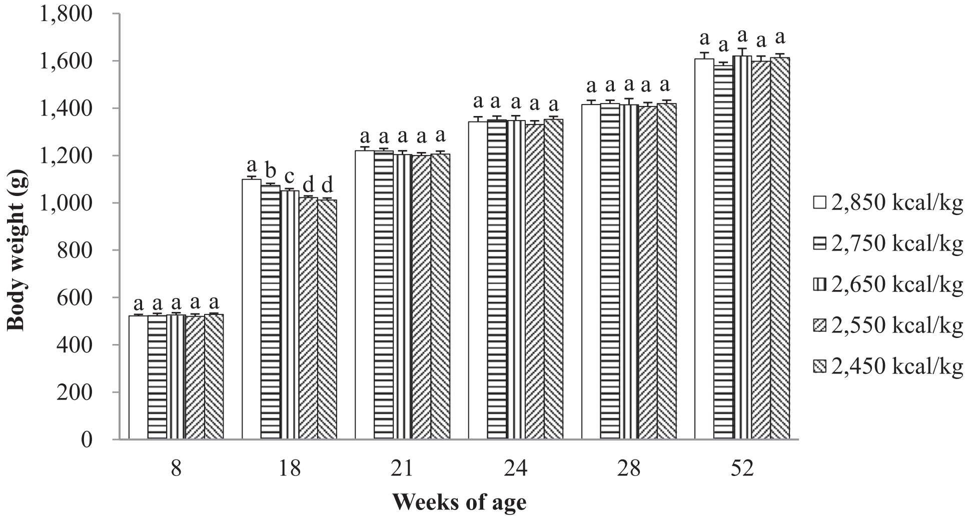

Figure 1. Effects of energy-restricted feeding from 8 to 18 wks of age on the BW (g) of Rugao layer breeders.[1]. [1]Values are means of 8 replicates per dietary treatment. Columns with different superscripts (a, b, c, d) at the same age are significantly different at $P < 0.05$.

the switch to basal diets for 3 wks (21 wks of age; $P = 0.290$). Although relatively few studies have investigated energy restriction during the rearing period on BW of laying hens, the BW of broilers in the feed-restricted groups was reduced at the end of the restriction period, and the difference in BW disappeared within 1 k after the feed restriction period for feed-restricted broilers during the second or third week of life (van der Klein et al., 2017). In addition, Urdaneta-Rincon and Leeson (2002) have shown that feed restriction of 10% from day 14 to 17, 20, 23, 26, or 29 reduced the BW of male broilers at d 35, but not d 42 or 49. In the present study, the energy intake of layer breeders during the rearing period (from 8 to 18 wks of age) was so low that even though the feed intake (nutrient intake) increased after the laying hens were switched to ad libitum feeding for 1 (63.55, 64.20, 67.03, 69.32, and 74.93; $P < 0.001$; data not shown) or 2 (64.97, 69.18, 69.45, 67.65, and 71.82; $P = 0.024$; data not shown) weeks, the difference in the BW between the energy-restricted feeding and ad libitum feeding groups remained. After the switch to basal diets, the growth of the laying hens was promptly compensated following a period of energy restriction, and the BW caught up at 3 wks after the restriction period. The results indicated that energy-restricted feeding adversely affected BW at the end of the restriction period, but the laying hens had the ability to catch up to the BW of hens in the ad libitum feeding group after the switch to ad libitum feeding.

The BW CV of laying hens decreased linearly with increasing energy restriction at 18 (L, $r^2 = 0.828$, $P = 0.032$; Q, $r^2 = 0.963$, $P = 0.037$), 21 (L, $r^2 = 0.953$, $P = 0.004$; Q, $r^2 = 0.995$, $P = 0.005$), and 24 (L, $r^2 = 0.857$, $P = 0.024$) weeks of age. No significant difference was observed in BW CV at 28 or 52 wks of age. A low BW CV indicates high flock uniformity, as it is an indirect measurement of uniformity. Available data on the influence of energy-restricted feeding during rearing phases on flock uniformity of laying hens were very limited for comparison with the results of the present study.

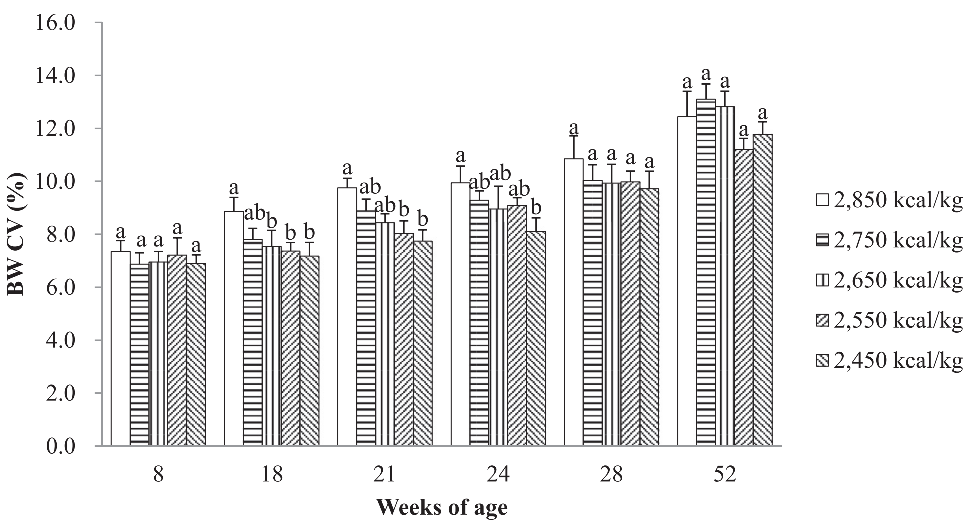

Figure 2. Effects of energy-restricted feeding from 8 to 18 wks of age on BW CV (%) of Rugao layer breeders.[1]. [1]Values are means of 8 replicates per dietary treatment. Columns with different superscripts (a, b) at the same age are significantly different at $P < 0.05$.

In broiler breeders, qualitative diet dilution and skip-a-day management did little to increase flock uniformity relative to the control group during the most intense period of feed restriction (7−19 wks of age), but skip-a-day treatment, as compared with qualitative dilution treatment, improved flock uniformity at 22 wks of age (Zuidhof et al., 2015). de Beer and Coon (2007) also reported an increase in flock uniformity of broiler breeders by skip-a-day feeding versus everyday limited feeding. Considerable evidence suggests that flock uniformity is affected by maintenance nutritional requirements, which fluctuate with the degree of feed restriction, age, and environmental temperature (Pishnamazi et al., 2015; Zuidhof et al., 2017). In this trial, energy restriction from 8 to 18 wks of age might have influenced nutrition absorption efficiency, thereby affecting the maintenance energy requirement, resulting in higher BW uniformity. High flock uniformity around the time of sexual maturation is desirable because laying hens that are uniform in BW should be more uniform in the onset of production, whereas poor uniformity is difficult to improve by simply adjusting feed and lighting. Furthermore, high flock uniformity is expected to increase lay persistency in layer breeder flocks (Bestman et al., 2012).

Visual Observations and Performance

From 18 to 52 wks of age, the egg number, laying rate, and egg mass showed a decreasing and then increasing quadratic response to increasing energy restriction from 8 to 18 wks of age ($P = 0.004$, 0.004, and 0.001, respectively; Table 4). Egg weight increased linearly as the degree of energy restriction increased ($P < 0.001$). FCR per kg and per dozen eggs, energy efficiency, and CP efficiency showed an increasing and then decreasing quadratic response to increasing energy restriction ($P = 0.001$, 0.004, 0.002, and 0.001, respectively). No differences were detected in the consumption of feed, AME and CP, peak of weekly laying rate, or mortality among the treatments. The data indicated that increasing energy restriction from 8 to 18 wks of age resulted in increased egg weight, without adverse effects on FCR, energy efficiency, and CP efficiency. Fuller and Chaney (1974) reported that energy-restricted feeding (2/3 energy of that in the ad libitum feeding diet) from 6 wks of age to the age at laying of the first egg resulted in increased egg weight and improved FCR in White Leghorn chickens, without affecting total egg number. Bruggeman et al. (1999) also reported that restricted feeding from 7 to 15 wks of age led to increased cumulative egg production and settable eggs as compared with ad libitum feeding in female Hybro G broiler breeders. In the current research, energy-restricted feeding did not increase egg number, laying rate, egg mass, FCR, energy efficiency, or CP efficiency as compared with those of hens in the ad libitum feeding group. These results indicate that greater feed restriction from 8 to 18 wks of age may have increased productive performance as in the cited previous studies. Egg weight increased as the energy restriction levels increased, suggesting that the productive performance was affected by the degree of energy restriction during the rearing period. During the energy restriction period, the maintenance nutritional requirements might have been lower in hens in the more severe energy restriction groups, thereby directing more nutrients toward the development of the reproductive system, resulting in much heavier eggs. However, further studies are needed to determine the reason the best performance was achieved by hens in the most severe energy restriction group.

Table 4. Effects of energy-restricted feeding from 8 to 18 weeks of age on productive performance of Rugao layer breeders from 18 to 52 wks of age[1].

	Control	Energy-restricted feeding(9−18 wks)					*P* value		
AME_n, kcal/kg	2,850	2,750	2,650	2,550	2,450	SEM	Energy restriction level	Linear	Quadratic
Egg number (n)	161.98[a]	158.47[ab]	155.81[b]	155.16[b]	159.17[ab]	0.746	0.019	0.067	0.004
Laying rate (%)	68.06[a]	66.58[ab]	65.46[b]	65.20[b]	66.88[ab]	0.313	0.019	0.067	0.004
Peak of weekly laying (%)	88.30	87.16	86.94	86.68	87.46	0.360	0.680	0.411	0.224
Egg weight (g)	41.83[b]	41.87[b]	42.62[a]	42.10[ab]	42.79[a]	0.090	<0.001	<0.001	0.964
Egg mass (g/ day)	28.47[ab]	27.88[bc]	27.90[bc]	27.44[c]	28.61[a]	0.118	0.006	0.832	0.001
Feed consumption (g/hen per day)	95.83	95.72	95.85	95.45	93.75	0.405	0.435	0.131	0.281
Feed conversion ratio (kg of feed/ kg of eggs)	3.37[ab]	3.44[a]	3.44[a]	3.48[a]	3.28[b]	0.020	0.007	0.277	0.001
Feed conversion ratio (kg of feed /dozen eggs)	1.69[ab]	1.73[ab]	1.76[a]	1.76[a]	1.68[b]	0.011	0.049	0.829	0.004
AME_n consumption (kcal/hen per day)	259.04	258.73	259.09	258.02	253.43	1.093	0.440	0.133	0.283
Energy efficiency (kcal of AME/ g of eggs)	9.10[ab]	9.28[a]	9.29[a]	9.40[a]	8.86[b]	0.054	0.008	0.287	0.002
Crude protein consumption (g/hen per day)	15.84	15.82	15.85	15.78	15.50	0.067	0.445	0.135	0.282
Crude protein efficiency (g of crude protein / g of egg)	0.56[ab]	0.57[a]	0.57[a]	0.58[a]	0.54[b]	0.003	0.005	0.277	0.001
Mortality (%)	3.14	1.82	2.23	1.37	1.82	0.447	0.793	0.350	0.561

[a,b]Means without common superscripts within a row differ significantly ($P < 0.05$).
[1]Values are means of eight replicates per dietary treatment.

Sexual Organ Development

The development of sexual organs at 18, 20, 22, 24, 26, and 28 wks of age are shown in Table 5. The number of large yellow follicles decreased as the energy restriction levels increased at 18 (L, $r^2 = 0.946$, $P = 0.005$; Q, $r^2 = 0.972$, $P = 0.028$), 20 (L, $r^2 = 0.838$, $P = 0.029$; Q, $r^2 = 0.997$, $P = 0.003$), and 22 (L, $r^2 = 0.839$, $P = 0.029$) wks of age, respectively. Likewise, the large yellow follicle index decreased as the energy restriction levels increased at 18 (L, $r^2 = 0.880$, $P = 0.018$; Q, $r^2 = 0.974$, $P = 0.026$) and 22 (L, $r^2 = 0.848$, $P = 0.026$) wks of age, respectively. Furthermore, the oviduct length decreased as the energy restriction levels increased at 18 (L, $r^2 = 0.865$, $P = 0.022$) and 20 (L, $r^2 = 0.852$, $P = 0.025$; Q, $r^2 = 0.959$, $P = 0.041$) wks of age, respectively, and the oviduct length index decreased as the energy restriction levels increased at 18 (L, $r^2 = 0.845$, $P = 0.027$) and 20 (L, $r^2 = 0.821$, $P = 0.034$) wks of age, respectively. The oviduct index decreased as the energy restriction levels increased at 18 (L, $r^2 = 0.921$, $P = 0.010$) and 20 (L, $r^2 = 0.899$, $P = 0.014$; Q, $r^2 = 0.997$, $P = 0.003$) wks of age, respectively. In addition, the ovary stroma index decreased as the energy restriction levels increased at 18 (L, $r^2 = 0.809$, $P = 0.038$; Q, $r^2 = 0.809$, $P = 0.038$), 20 (L, $r^2 = 0.749$, $P = 0.048$), and 22 (L, $r^2 = 0.782$, $P = 0.046$) wks of age, respectively. Laying hens in the most severe energy-restricted feeding group had lighter sexual organs than hens in the ad libitum feeding and lighter energy-restricted feeding groups at 24 wks of age ($P < 0.05$). However, the sexual organ development of laying hens was not affected by energy restriction during the rearing period at 26 or 28 wks of age.

The development of sexual organs of broiler breeders can be controlled with feed restriction (Hocking et al., 1993; Renema et al., 1999), which slows the growth rate of the follicle and oviduct (Bruggeman et al., 1999). Therefore, feed restriction programs are used to delay the development of sexual organs and to prevent premature sexual maturity (Renema and Robinson, 2004). The results of laying hens in this trial were in accordance with the results of broiler breeders in the cited studies. In the present study, energy-restricted feeding was conducted until 18 wks of age. After energy restriction, the BW of the hens began to increase, which ensured that most were physically mature, then to reach sexual maturity. Once body growth slows down after reaching an adequate BW, the oviduct and ovary begin to grow

Table 5. Effects of energy-restricted feeding from 8 to 18 wks of age on the development of sexual organs at 18, 20, 22, 24, 26, and 28 wks of age.[1]

Item	Week	Control 2,850	Energy-restricted feeding (9−18 wks) 2,750	2,650	2,550	2,450	SEM	*P* value: Energy restriction level	Linear	Quadratic
Large yellow follicles (n)	18	1.63[a]	0.88[b]	0.63[bc]	0.38[c]	0.00[d]	0.150	0.017	0.005	0.028
	20	2.38[a]	2.50[a]	2.13[ab]	1.63[b]	0.75[c]	0.200	0.036	0.029	0.003
	22	4.25[a]	3.88[a]	4.00[a]	2.75[b]	2.63[b]	0.225	0.027	0.029	0.137
	24	3.88[ab]	4.13[a]	4.00[a]	4.75[a]	3.25[b]	0.132	0.030	0.762	0.541
	26	3.75	4.75	5.13	3.63	4.75	0.095	0.521	0.737	0.850
	28	4.25	4.50	4.63	4.38	4.63	0.074	0.923	0.270	0.526
Large yellow follicle index (%)	18	6.24[a]	3.47[b]	1.09[c]	1.10[c]	0.00[d]	0.559	0.019	0.018	0.026
	20	7.56[b]	9.73[a]	7.62[b]	4.21[c]	2.90[d]	0.744	0.022	0.073	0.189
	22	14.44[a]	11.20[b]	12.36[b]	8.16[c]	7.55[c]	0.725	0.038	0.026	0.152
	24	14.68[ab]	16.81[a]	13.24[ab]	18.54[a]	11.35[b]	0.544	0.046	0.754	0.884
	26	17.85	19.50	21.01	16.94	18.94	0.445	0.673	0.849	0.910
	28	16.41	17.23	19.01	16.72	17.64	0.391	0.868	0.736	0.571
Oviduct length (cm)	18	18.58[a]	15.34[ab]	13.26[b]	14.13[b]	9.96[c]	0.742	0.025	0.022	0.132
	20	28.43[a]	26.71[a]	25.83[a]	23.99[ab]	17.70[b]	1.232	0.018	0.025	0.041
	22	38.70[a]	34.34[ab]	34.90[ab]	28.58[b]	31.43[ab]	1.408	0.037	0.074	0.222
	24	48.94[a]	46.78[a]	46.46[a]	49.15[a]	37.03[b]	0.891	0.048	0.266	0.508
	26	46.85	51.04	50.95	44.93	50.36	0.739	0.607	0.468	0.716
	28	52.10	52.88	50.26	53.61	51.06	0.317	0.477	0.768	0.898
Oviduct length index (cm/kg)	18	18.13[a]	13.86[b]	12.89[b]	13.21[b]	9.28[c]	0.693	0.014	0.027	0.148
	20	23.64[a]	21.87[a]	22.07[a]	19.94[ab]	14.89[b]	1.000	0.027	0.034	0.056
	22	32.12[a]	25.40[b]	26.94[b]	22.22[c]	23.78[c]	1.101	0.016	0.085	0.188
	24	35.85[a]	35.19[a]	35.07[a]	37.52[a]	28.40[b]	0.682	0.026	0.405	0.752
	26	36.67	39.31	37.52	36.61	34.88	0.602	0.853	0.766	0.546
	28	38.93	37.53	35.59	36.77	38.24	0.301	0.463	0.619	0.089
Oviduct index (%)	18	6.78[a]	3.91[b]	3.77[b]	2.67[c]	0.48[d]	0.562	0.029	0.010	0.079
	20	13.41[a]	12.98[a]	11.58[b]	7.98[c]	3.97[d]	0.894	0.025	0.014	0.003
	22	21.64[a]	14.30[c]	18.37[b]	12.20[d]	11.92[d]	0.968	0.021	0.097	0.331
	24	18.95[a]	20.42[a]	19.14[a]	19.08[a]	14.70[b]	0.543	0.038	0.177	0.081
	26	23.02	21.99	23.09	22.09	21.10	0.387	0.932	0.482	0.809
	28	25.24	24.05	23.65	26.57	22.89	0.353	0.521	0.666	0.784
Ovary stroma index (%)	18	0.55[a]	0.57[a]	0.48[b]	0.47[b]	0.45[b]	0.018	0.017	0.038	0.038
	20	0.75[a]	0.55[b]	0.56[b]	0.45[c]	0.48[c]	0.022	0.021	0.048	0.072
	22	1.15[ab]	1.32[a]	0.90[bc]	0.77[c]	0.68[c]	0.056	0.004	0.046	0.204
	24	1.62[ab]	2.03[a]	1.33[b]	1.74[ab]	1.26[b]	0.055	0.015	0.314	0.175
	26	2.15	2.27	2.11	1.73	1.74	0.046	0.024	0.827	0.051
	28	2.29	2.24	2.55	2.00	2.14	0.039	0.253	0.331	0.455

[a,b]Means without common superscripts within a row differ significantly (P < 0.05).
[1]Values are means of eight replicates per dietary treatment.

(Bédécarrats, 2015). Therefore, hens in the ad libitum feeding groups were physically mature earlier and the sexual organs developed earlier as compared with those of hens in the energy-restricted feeding groups. Furthermore, differences in sexual organ development were observed at 18, 20, 22 and 24 wks of age, but not at 26 or 28 wks of age, suggesting that the effect of energy-restricted feeding during rearing on sexual organ development can be substantial during sexual maturity, but disappears with aging.

Sexual Maturity

Sexual maturity variables of laying hens administered different degrees of energy restriction from 8 to 18 wks of age are shown in Table 6. The ages of laying the first egg and at 5% and 50% egg production increased linearly as the degree of energy restriction increased ($P = 0.042$, 0.004, and 0.029, respectively). The interval from 5% to 50% egg production showed a decreasing and then increasing quadratic response to increasing energy restriction ($P = 0.003$). Egg number from 5% to 50% egg production decreased linearly as the energy restriction levels increased ($P = 0.001$). BW at the age of laying the first egg, age at 80% egg production, intervals from 50% to 80% and 5% to 80% egg production, egg numbers from 50% to 80%, 5% to 80%, and above 80% egg production were not affected by energy restriction. Energy-restricted feeding (2/3 energy of that in the ad libitum feeding diet) from 6 wks of age to the age at laying the first egg delayed sexual maturity by 3 wks in spring-reared White Leghorn chickens (Fuller and Chaney, 1974). In addition, both feed restriction from 7 to 15 wks of age and from 7 wks of age to the age at laying the first egg led to a later age at laying the first egg in female Hybro G broiler breeders (Bruggeman et al., 1999). In this trial, energy-restricted feeding delayed the age at laying the first egg and age at 5% and 50% egg production by 4.2, 8.9 and 5.5 d, respectively, and decreased the egg number from 5% to 50% egg production by 4.4. The results indicated that greater feed restriction from 8 to 18 wks of age may have delayed sexual maturity as reported in the above studies. After the energy restriction period, the BW of the hens began to increase. Once an adequate BW was reached, the sexual organs developed and sexual maturation hastened. The difference in BW between the energy-restricted feeding and ad libitum feeding hens disappeared until the laying hens were switched to ad libitum feeding for 3 wk. Thus, the sexual maturity of laying hens administered with energy-restricted feeding was delayed.

Reproductive Performance

Fitting of laying rate curves of hens in ad libitum feeding and energy-restricted feeding treatments is shown in Figure 3. The fitting of rate curves are as follows:

$$2,850\ kcal/kg : y(t) = 125.5621 \times e^{-0.0119\times t} / \left[\left(1 + e^{-0.4733\times(t-23.5684)}\right)\right], R^2 = 0.9947$$

$$2,750\ kcal/kg : y(t) = 113.3551 \times e^{-0.0097\times t} / \left[\left(1 + e^{-0.6512\times(t-23.7046)}\right)\right], R^2 = 0.9947$$

$$2,650\ kcal/kg : y(t) = 120.8847 \times e^{-0.0114\times t} / \left[\left(1 + e^{-0.6128\times(t-24.1779)}\right)\right], R^2 = 0.9933$$

$$2,550\ kcal/kg : y(t) = 129.1393 \times e^{-0.0132\times t} / \left[\left(1 + e^{-0.5640\times(t-24.1191)}\right)\right], R^2 = 0.9938$$

$$2,450\ kcal/kg : y(t) = 116.1368 \times e^{-0.0098\times t} / \left[\left(1 + e^{-0.6379\times(t-24.1069)}\right)\right], R^2 = 0.9941$$

Egg production of hens in the energy-restricted feeding groups was lower than that of hens in the ad libitum feeding group (6.36, 6.43, 6.4, and 4.61% vs. 14.29%) in the first period (18 to 20 weeks of age; $P < 0.05$; data not shown). In addition, egg production of hens in the 2,650 and 2,450 kcal AME_n/kg groups was lower than that of hens in the ad libitum feeding group (26.29 and 25.96%

Table 6. Effects of energy-restricted feeding from 8 to 18 wks of age on sexual maturity variables of Rugao layer breeders.[1]

	Control	Energy-restricted feeding (8–18 wk)					P value		
AME_n, kcal/kg	2,850	2,750	2,650	2,550	2,450	SEM	Energy restriction level	Linear	Quadratic
Age at first egg (day of age)	151.40[d]	152.65[c]	152.85[c]	154.57[b]	155.64[a]	0.638	0.034	0.042	0.808
BW at first egg (g)	1,305.18	1,293.52	1,283.84	1,293.04	1,304.06	5.852	0.791	0.935	0.210
Age at 5% egg production (day of age)	122.00[b]	128.00[ab]	131.25[a]	131.50[a]	130.88[a]	1.094	0.020	0.004	0.056
Age at 50% egg production (day of age)	166.38[b]	165.75[b]	169.00[ab]	165.50[b]	171.88[a]	0.859	0.043	0.029	0.291
Age at 80% egg production (day of age)	191.13	191.88	194.63	196.75	194.88	2.125	0.927	0.435	0.753
5% to 50% egg production interval (day)	44.38[a]	37.75[bc]	37.75[bc]	34.00[c]	41.00[ab]	0.993	0.008	0.095	0.003
50% to 80% egg production interval (day)	24.75	26.13	25.63	31.25	23.00	1.981	0.765	0.911	0.447
5% to 80% egg production interval (day)	69.13	63.88	63.38	65.25	64.00	2.297	0.942	0.604	0.609
5% to 50% egg production egg number (n)	11.20[a]	7.50[b]	7.98[b]	7.33[b]	6.81[b]	0.425	0.004	0.001	0.093
50% to 80% egg production egg number (n)	16.83	17.96	17.80	21.35	18.76	1.518	0.917	0.520	0.779
5% to 80% egg production egg number (n)	28.01	25.45	25.80	28.68	25.56	1.610	0.955	0.889	0.920
Above 80% egg production egg number (n)	68.06	62.08	51.65	47.26	59.51	3.270	0.278	0.169	0.123

[a-d]Means without common superscripts within a row differ significantly ($P < 0.05$).
[1]Values are means of eight replicates per dietary treatment.

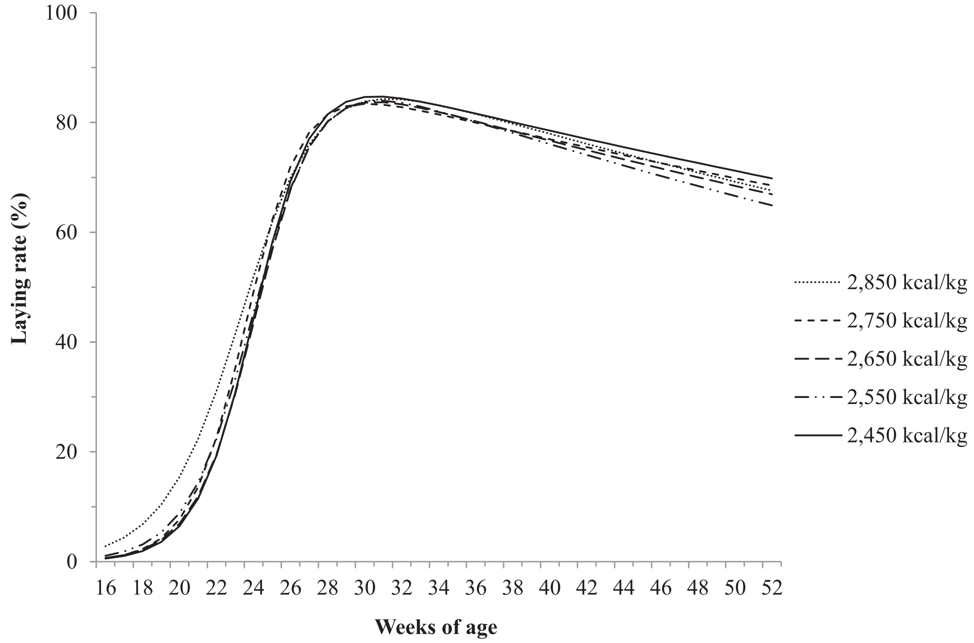

Figure 3. Effects of energy-restricted feeding from 8 to 18 wks of age on laying rate curves of Rugao layer breeders.[1]. [1]Values are means of 8replicates per dietary treatment.

vs. 36.84%) in the second period (20 to 24 wks of age; $P < 0.05$; data not shown). Furthermore, egg production of hens in the 2,450 kcal AME_n/kg group was highest after peak laying, which was higher than that of hens in the 2,550 kcal AME_n/kg group from 44 to 48 (74.50% vs. 68.99%; data not shown) and from 48 to 52 (70.30% vs. 65.18%; data not shown) wks of age ($P < 0.05$).

In the present study, the mean age of sexual maturity increased (23.57, 23.70, 24.18, 24.12, and 24.11 wks of age) as the degree of energy restriction during rearing increased, which was consistent with the data of sexual organ development and sexual maturity variables. After energy restriction, hens in the energy-restricted feeding groups began to grow and reached physically maturity and then sexual maturity. Therefore, sexual organ development, age at laying the first egg, and age at 5% and 50% egg production were delayed, and the egg production was very low in the first 2 periods. Then, the laying rate of hens in the energy-restricted feeding groups increased quickly after 21 wks of age when the difference in BW among the treatments disappeared and the laying rate of hens in the most severe energy restriction group decreased slowly after peak laying. Energy-restricted feeding increased reproductive performance throughout the laying period because of complete development of the reproductive system, which increased the recruitment rate of large yellow follicles and decreased the incidence of follicular atresia, internal ovulation, and the membrane production of soft-shelled eggs (Morris and Perry, 2002; Tyler and Gous, 2012). The relatively high flock uniformity in BW and physically maturity of hens in the energy-restricted groups might be another means to induce hens to commence laying within a narrow range of time and start production as a more uniform flock. However, further studies are needed to determine why hens in the most severe energy restriction group achieved higher performance than those in the lighter energy-restricted feeding groups.

Setting Egg Number, Fertility, and Hatchability

The number of eggs weighing more than and less than 40 g are presented in Figure 4. For the entire experimental period, the number of eggs weighing <40 g decreased linearly as the degree of energy restriction in the rearing period increased (17.64, 15.81, 12.18, 13.38, and 9.60; L, $r^2 = 0.874$, $P = 0.020$). Small eggs were produced mostly in the first 2 laying periods (18−24 wks of age; data not shown). Furthermore, laying hens in the most severe energy restriction group laid more eggs weighing >40 g than hens in the ad libitum feeding and lighter energy-restricted feeding groups (149.57 vs. 144.34, 142.66, 143.63, and 141.78; $P < 0.05$). Eggs weighing > 40 g can be used as setting eggs of native layer breeders in the Chinese layer breeder industry. In this trial, laying hens in the most severe energy restriction group laid the least small eggs and the most setting eggs. This is in agreement with the finding of Fuller and Chaney (1974) that energy-restricted feeding (2/3 energy of that in the ad libitum feeding diet) from 6 wks of age to the age at laying the first egg resulted in an increase in the number of settable eggs and lager eggs produced by White Leghorn chickens. In broiler breeders, overfeeding during the rearing phase is very likely to result in excessive production of large yellow follicles that are more likely to be organized in multihierarchies (Hocking et al., 1989; Katanbaf et al., 1989; Renema et al., 1999), which is corrected through the implementation of feed restriction programs, resulting in an increase in the amount of

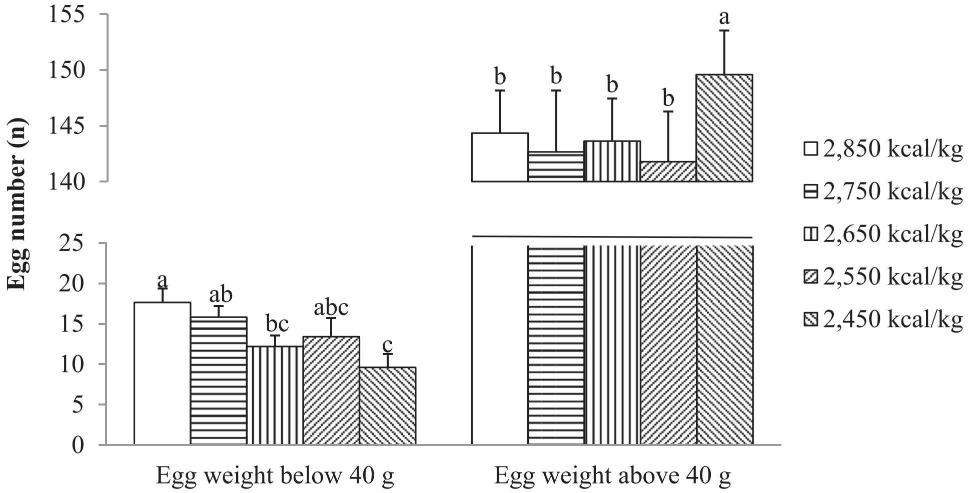

Figure 4. Effects of energy-restricted feeding from 8 to 18 wks of age on egg number (n) of Rugao layer breeders.[1]. [1]Values are means of 8 replicates per dietary treatment. Columns with different superscripts (a, b, c) are significantly different at $P < 0.05$.

Table 7. Effects of energy-restricted feeding from 8 to 18 weeks of age (in rearing period) on fertility and hatchability of Rugao layer breeders at 52 wks of age[1].

	Control	Energy-restricted feeding (9–18 wks)					*P* value		
AME_n, kcal/kg	2,850	2,750	2,650	2,550	2,450	SEM	Energy restriction level	Linear	Quadratic
Fertility	93.89	93.78	94.25	93.99	95.07	0.532	0.381	0.910	0.774
Hatchability of fertile eggs	91.22	89.88	92.17	90.77	91.77	0.655	0.790	0.517	0.282
Hatchability of setting eggs	85.65	84.79	87.22	85.57	88.09	0.708	0.605	0.243	0.357

[1]Values are means of 8 replicates per dietary treatment.

setting eggs (Hocking et al., 1987; Yu et al., 1992). In the present study, therefore, energy-restricted feeding delayed both physical and sexual maturity, increased the duration of reproductive system development, decreased the egg number from 5% to 50% egg production, and resulted in larger numbers of setting eggs.

As shown in Table 7, there were no statistically significant differences in fertility, hatchability of fertile eggs, or hatchability of setting eggs in either the control or treatment group ($P = 0.381$, 0.790, and 0.605, respectively). The performance of energy-restricted feeding on fertility and hatchability was in agreement with that found by Katanbaf et al. (1989) and Wilson et al. (1989), who found no difference in hatchability between the daily restriction and skip-a-day restriction broiler breeders. Furthermore, de Beer and Coon (2007) reported no difference in hatchability among broiler breeders subjected to the daily, skip-a-day, 4/3, and 5/2 restriction programs. These results suggested that the effect of energy-restricted feeding from 8 to 18 wks of age results primarily in delayed sexual maturity and an increase in the number of setting eggs rather than in further influence on fertility and hatchability.

In conclusion, the findings of the present study revealed that moderate energy restriction (85.97%, 2,450 vs. 2,850 kcal AME_n/kg) from 8 to 18 ks of age could increase BW uniformity in the early laying period, delay sexual organ development and sexual maturity, while increasing the average egg weight as well as the production of setting eggs of layer breeders throughout the laying period, without adverse effects on productive performance, fertility, and hatchability. These results provide a theoretical basis for the application of energy-restricted feeding in layer breeders.

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DISCLOSURES

The authors declare that there are not any conflicts of interest.

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