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Effects of energy restriction during growing phase on the productive performance of Hyline Brown laying hens aged 6 to 72 wk

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ABSTRACT The aim of this study was to assess the effects of energy-restricted feeding during growing phase on the productive performance of Hyline Brown laying hens aged 6 to 72 wk. A total of 720 six-week-old layer chicks were allocated equally to 3 groups with 6 replicates of 40 pullets each, and were fed 1 of 3 diets that were nutritionally similar except for the apparent metabolizable energy corrected for nitrogen (**AME$_n$**) content. At the age of 6 to 17 wk, the pullets in the control group were given diet with 2,850 kcal/kg AME$_n$, and were fed ad libitum. The levels of AME$_n$ in diet of pullets in the experimental groups were 90% (2,565 [2,850 × 90%] kcal/kg) and 80% (2,280 [2,850 × 80%] kcal/kg) of that in control group, and the daily amount of feed was restricted to the absolute quantity of the diet consumed by pullets in control group. At the age of 18 to 72 wk, all the hens were fed with the same diets ad libitum. As energy restriction increased in the growing phase, body weight (**BW**) dropped at the ages of 12 and 15 to 23 wk (at 23 wk: $P = 0.001$; at other ages: $P < 0.001$), but it showed no significant difference at 24 wk ($P = 0.071$). At 20 wk, restricting energy induced a delay in the development of sexual organs, including the ovary stroma, oviduct, and small yellow follicle ($P < 0.05$), as well as a delay in sexual maturity ($P < 0.05$). Consequently, the laying rate in the first and second periods dropped linearly ($P = 0.046$, 0.030, and 0.038, $P < 0.001$, respectively). The coefficient of variation (**CV**) in the BW at 19, 20, and 21 wk ($P = 0.040$, 0.023, and 0.042, respectively), the CV of age at first egg ($P < 0.001$), and CV of individual egg number at age 18 to 72 wk ($P < 0.001$) decreased linearly. There was a linear increase in the laying rate of hens in the later periods (at age 32−72 wk, $P < 0.05$), as well as in the average total egg number per hen and average laying rate at the age of 18 to 72 wk ($P = 0.006$). The average egg mass also showed a linear increase with increasing levels of energy restriction ($P < 0.001$). In summary, although appropriate energy restriction during growing phase delayed sexual maturity and sexual organ development in early-laying Hyline Brown pullets, it improved uniformity of BW, age at first egg laying, and individual egg number, and increased egg number per hen, laying rate, average egg mass, and number of settable eggs from 18 to 72 wk of age.

Key words: laying hen, energy consumption during growing phase, productive performance, sexual organ development, sexual maturity

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INTRODUCTION

The growing phase is a pivotal phase during a laying hen's lifetime as it is when evident growth occurs in body size, skeleton, and reproductive organs. Any disruption in management strategies during this period cannot be corrected later (Bestman et al., 2012), making this period all the more crucial. The growth and development status of pullets during this period are important factors affecting physical maturity and sexual maturity, which, in turn, determines their performance during the entire laying period (Bestman et al., 2012). Thus, it is vital to attain the desired body weight (**BW**), high flock uniformity, and proper development of organs before the transfer of pullets into the laying house.

If laying hens have low rather than excess BW at the beginning of their laying cycle, they will produce fewer and smaller eggs throughout the entire cycle (Leeson

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et al., 1997; Pérez-Bonilla et al., 2012a,b). It is vital to have good flock uniformity before the laying period starts to achieve maximum production, as both overweight and underweight hens have suboptimal performance (Bestman et al., 2012). Discrepant feeding strategies have been utilized to optimize the BW of broiler breeders for better reproductive performance. Among them, dietary restriction techniques during growing phase have been found to increase the overall egg production, settable eggs, and average egg weight, and enhance fertility, hatchability, and egg quality in broiler breeders (Zuidhof, 2018; Heijmans et al., 2021; Avila et al., 2023). These benefits imply that comparable feeding management practices may be adopted for laying hens to decelerate the development of their reproductive system, postpone sexual maturity, and enhance their egg-laying performance. In a previous study on Rugao layer breeders, we observed that restricting energy intake in the growing phase increased the number of setting eggs and egg weight, even though it delayed sexual maturity (Lu et al., 2021).

Despite these findings, there is a scarcity of research that emphasizes the improvement of laying performance during the subsequent laying period. The hypothesis tested in this study was that energy-restricted feeding in the earlier growing phase might improve flock uniformity of young layer breeders and the subsequent laying performance, but adversely affect BW and delayed sexual maturity and sexual organ development in early-laying period. Therefore, the aim of this study was to examine how low energy consumption at age 6 to 17 wk affects the laying performance of Hyline Brown hens at 18 to 72 wk.

MATERIALS AND METHODS

Study Design, Birds, and Diets

A total of 720, six-wk-old, Hyline Brown layer chicks were assigned equally to 3 groups with 6 replicates of 40 pullets each, and were fed 1 of 3 diets that were nutritionally similar except for the apparent metabolizable energy corrected for nitrogen (**AME$_n$**) content. At the age of 6 to 17 wk, the pullets in the control group were given diet with 2,850 kcal/kg AME$_n$, and fed ad libitum. The levels of AME$_n$ in the diet of pullets in the experimental groups were 90% (2,565 [2,850 × 90%] kcal/kg) and 80% (2,280 [2,850 × 80%] kcal/kg) of that in the control group (Table 1), and the daily amount of feed was restricted to the absolute quantity of the diet consumed by pullets in control group. At the age of 18 to 72 wk, all hens were fed the same basal diet ad libitum (Table 2) formulated to meet the National Research Council (1994) recommendations for laying hens. The experiment lasted from 6 to 72 wk of age.

Husbandry

This trial was performed at the Poultry Institute of the Chinese Academy of Agricultural Sciences (Yangzhou City, Jiangsu, China) from August 2021 to December 2022. At the age of 6 to 17 wk, pullets were weighed individually and then placed in cages in groups through random allocation. At the age of 18 to 72 wk, all hens were kept in a laying house, with each hen housed individually. Light exposure followed the light program recommended by Hyland International Breeding Company, which involved 12 h of light at the age of 6 to 7 wk, 10 h at 7 to 17 wk, and a gradual increase to 16 h at 30 wk. All animal handling protocols were approved by the Animal Care and Use Committee of the Poultry Institute (SYXK(Su)IACUC 2012-2029).

Sample Collection and Analytical Determination

BW and Uniformity. The chicks' BW was measured individually on a weekly basis at the age of 6, 12, 15, 17 to 24 wk, and 27 wk. For the assessment of BW uniformity, the coefficient of variation (**CV**) was utilized as an indirect measure (Peak et al., 2000; Guzmán et al., 2016). CV = (standard deviation/average BW) × 100%.

Growth Performance. The feed consumption by replicate was measured weekly. The average daily weight gain (**ADG**), average daily feed intake (**ADFI**), feed conversion ratio (**FCR**), and AME$_n$ consumption were determined by period and cumulatively.

Sexual Organ Development. At 15, 17, 20, 24, 28, 36, and 72 wk of age, 2 hens from each replicate were humanely sacrificed. This experiment involved the measurement of the number of small yellow follicles (4−8 mm diameter), large white follicles (2−4 mm diameter), and preovulatory follicles (>8 mm diameter), as well as the length of the oviduct following the method of Lu et al. (2021). Additionally, the weights of large white follicles, small yellow follicles, preovulatory follicles, oviducts (emptied of contents), and ovary stroma were recorded.

Estradiol and Progesterone Hormone. With the aim of obtaining 1.5 mL of blood samples, 2 birds were bled from each replicate. All samples were immediately centrifuged to collect the serum. The estradiol and progesterone concentrations were assayed directly with a commercial kit (Nanjing AngleGene Biotech Co. Ltd., Nanjing, China).

Sexual Maturity. Individual daily egg counts per hen were recorded, and the BW at first egg laying was documented. The age at which each replicate attain the laying rates of 5%, 50%, and 90% was calculated.

Productive Performance. The daily egg production and weight of each hen were recorded, while the weekly feed intake was measured. The average egg weight, egg mass, laying rate (hen-day egg production), feed conversion ratio, feed intake, and energy efficiency were determined. Energy efficiency = kcal of AME/ g of eggs.

The laying rate curve model (Yang et al., 1989) was used:

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

where, $y(t)$ is the laying rate (%), t indicates age (wk), and a to d denote scale variable, rate of decline in laying

Table 1. Ingredients and nutrient levels of the experimental diet provided from 6 to 17 wk of age.[1]

AME_n, kcal/kg	6–12 wk			12–17 wk		
	Control	Energy-restricted feeding		Control	Energy-restricted feeding	
	2,850	2,565	2,280	2,850	2,565	2,280
Ingredient (%)						
Corn	71.11	61.00	50.20	75.20	64.80	54.30
Soybean meal	25.67	27.60	29.40	20.80	22.70	24.50
Limestone	1.40	1.40	1.40	2.00	2.00	2.00
Zeolite powder	—	8.23	17.26	0.20	8.75	17.49
Dicalcium phosphate	0.105	0.105	0.105	0.105	0.105	0.105
Monocalcium phosphate	0.595	0.595	0.595	0.595	0.595	0.595
Sodium chloride	0.25	0.25	0.25	0.25	0.25	0.25
50% choline chloride	0.12	0.12	0.12	0.10	0.10	0.10
DL-methionine	0.15	0.16	0.17	0.15	0.15	0.16
Lysine	0.10	0.04	—	0.10	0.05	—
Vitamin and trace mineral premix [2]	0.50	0.50	0.50	0.50	0.50	0.50
Nutrient levels (calculated)[3]						
AME_n (kcal/kg)	2,850	2,565	2,280	2,850	2,565	2,280
Crude protein (%)	17.50	17.50	17.50	15.50	15.50	15.50
Total amino acid (%)						
Lysine	0.94	0.94	0.94	0.82	0.82	0.82
Methionine	0.45	0.45	0.45	0.41	0.41	0.41
Met + Cys	0.73	0.73	0.73	0.67	0.67	0.67
L-tryptophan	0.20	0.21	0.22	0.18	0.18	0.18
Threonine	0.66	0.66	0.66	0.59	0.59	0.59
Calcium (%)	0.80	0.80	0.80	0.80	0.80	0.80
Total phosphorus (%)	0.50	0.50	0.50	0.50	0.50	0.50
Nonphytate phosphorus (%)	0.27	0.27	0.27	0.27	0.27	0.27
Nutrient levels (measured)						
DM (%)	91.90	92.35	92.46	92.17	92.84	91.82
Gross energy (kcal/kg)	4,017	3,845	3,672	4,032	3,824	3,688
Crude protein (%)	17.75	17.59	17.63	15.61	15.58	15.58
Total amino acid (%)						
Lysine	0.89	0.87	0.87	0.78	0.76	0.79
Methionine	0.43	0.42	0.44	0.38	0.26	0.37
Met + Cys	0.74	0.73	0.71	0.69	0.67	0.66
L-tryptophan	0.19	0.20	0.19	0.19	0.17	0.18
Threonine	0.64	0.66	0.65	0.58	0.56	0.57
Calcium (%)	0.84	0.86	0.79	0.87	0.88	0.83
Total phosphorus (%)	0.53	0.49	0.51	0.53	0.51	0.51

[1]Values are expressed on an air-dry basis.
[2]Premix included (per kg of diet): vitamin A, 7,715 IU; vitamin D_3, 2,755 IU; vitamin E, 8.8 IU; cobalamin, 20 μg; riboflavin, 2.21 mg; nicotinic acid, 19.8 mg; pantothenic acid, 3.51 mg; menadione, 2.2 mg; folic acid, 0.28 mg; pyridoxine, 3.25 mg; thiamine, 0.65 mg; biotin, 0.20 mg; manganese, 65 mg; zinc, 80 mg; iron, 60 mg; copper, 8 mg; iodine, 1.0 mg; and selenium, 0.3 mg.
[3]According to Nutrition Parameter and Feeding Standard for Animals (Zhang, 2010).

ability, an inverse indicator of the variation in sexual maturity, and mean age at sexual maturity, respectively.

Diet Assays. Samples of diets were ground to pass through a 40-mesh sieve and immediately frozen and stored at −20°C for further analysis. Gross energy was determined with an adiabatic bomb calorimeter (Model 1356; Parr Instrument Company, Moline, IL). Crude protein, amino acid, calcium, and phosphorus were determined according to the procedures of AOAC International (2005).

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 the linear and quadratic relationships of the responses of hens to different energy restriction interventions. Significant differences were reported for $P < 0.05$.

RESULTS

Energy-Restricted Feeding Model

The consumption of AME_n decreased linearly at the ages of 6 to 12, 12 to 15, 15 to 17, and 6 to 17 wk (Table 3, $P < 0.001$), implying the successful modeling of the energy-restricted feeding in the growing phase.

BW and Uniformity

There was a linear decrease in the BW of hens at the ages of 12 and 15 to 23 wk with increasing energy

Table 2. Ingredients and nutrient levels of the experimental diet provided from 17 to 72 wk of age.[1]

	17–20 wk	20–72 wk
Ingredient (%)		
Corn	68.00	65.50
Soybean meal	24.00	23.50
Limestone	—	3.00
Calcareous granule	6.00	6.00
Zeolite powder	0.23	0.23
Dicalcium phosphate	0.105	0.105
Monocalcium phosphate	0.595	0.595
Sodium chloride	0.25	0.25
50% choline chloride	0.12	0.12
DL-methionine	0.20	0.20
Vitamin and trace mineral premix[2]	0.50	0.50
Nutrient levels (calculated)		
AME_n (kcal/kg)	2,800	2,700
Crude protein (%)	16.50	16.00
Total amino acid (%)		
Lysine	0.84	0.82
Methionine	0.47	0.47
Methionine + cystine	0.74	0.73
L-tryptophan	0.19	0.19
Threonine	0.62	0.61
Calcium (%)	2.60	3.80
Total phosphorus (%)	0.50	0.50
Nonphytate phosphorus (%)	0.27	0.27
Nutrient levels (measured)		
DM (%)	91.61	92.08
Gross energy (kcal/kg)	3,944	3,892
Crude protein (%)	16.59	16.04
Total amino acid (%)		
Lysine	0.81	0.79
Methionine	0.48	0.45
Met + Cys	0.75	0.70
L-tryptophan	0.20	0.18
Threonine	0.59	0.59
Calcium (%)	2.68	3.78
Total phosphorus (%)	0.51	0.54
	54	

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

[2]Premix included (per kg of diet): vitamin A, 7,715 IU; vitamin D_3, 2,755 IU; vitamin E, 8.8 IU; cobalamin, 20 μg; riboflavin, 2.21 mg; nicotinic acid, 19.8 mg; pantothenic acid, 3.51 mg; menadione, 2.2 mg; folic acid, 0.28 mg; pyridoxine, 3.25 mg; thiamine, 0.65 mg; biotin, 0.20 mg; manganese, 65 mg; zinc, 80 mg; iron, 60 mg; copper, 8 mg; iodine, 1.0 mg; and selenium, 0.3 mg.

restriction (at age 23 wk: $P = 0.001$; at other ages: $P < 0.001$) (Table 4). BW at age 24 wk (after the switch to free feeding for 7 wk) exhibited no significant difference ($P = 0.071$). The BW CV of pullets decreased linearly at the ages of 19 ($P = 0.040$), 20 ($P = 0.023$), and 21 ($P = 0.042$) wk.

Growth Performance

There was a decline in the ADG ($P < 0.001$) and an increase in the FCR ($P < 0.001$) with the elevated level of energy restriction at age 6 to 17 wk (Table 5). At age 20 to 24 wk, there was an upward trend in ADG ($P < 0.001$) and a downward trend in FCR ($P = 0.001$). A linear increase was observed in ADFI ($P = 0.005$) and FCR ($P = 0.001$) at age 6 to 24 wk.

Sexual Organ Development

Table 6 showed sexual organ development at ages 15, 17, 20, 24, 28, 36, and 72 wk. Decreases in the oviduct length, oviduct weight, oviduct length index, and oviduct index were observed with increasing energy restriction levels at age 20 wk ($P = 0.038$, 0.017, 0.041, and 0.025, respectively). Likewise, the weight ($P = 0.037$) and index ($P = 0.021$) of the ovary stroma decreased at age 20 wk. The number, weight, and index of small yellow follicles decreased at age 20 wk ($P = 0.035$, 0.017, and 0.047, respectively). No statistically significant difference was observed in the large white follicles and preovulatory follicles ($P > 0.05$).

Estradiol and Progesterone Hormones

The estradiol hormone levels in pullets increased linearly at age 15 and 17 wk ($P = 0.044$ and 0.031, respectively) but decreased linearly at age 18 and 19 wk ($P = 0.001$ and 0.006, respectively) as the degree of energy restriction increased (Table 7). The progesterone hormone levels of pullets receiving 80% energy-restricted feeding peaked at age 15 wk, but were lowest at 16 wk ($P < 0.05$; Table 8). In contrast to pullets in the groups receiving ad libitum feeding and the 80% energy-restricted feeding, those receiving 90% energy-

Table 3. Feed consumption (g/ pullet per day) and AME_n consumption (kcal AME_n/ pullet per day) of laying pullets from 6 to 17 wk of age.[1]

Items	Control	Energy-restricted feeding (6–17 wk)		SEM	*P*-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
6–12 wk							
Feed consumption	60.1	60.1	60.1	0.038	0.815	0.575	0.774
AME_n consumption	177.2[a]	159.5[b]	141.8[c]	14.641	<0.001	<0.001	0.948
12–15 wk							
Feed consumption	80.8	82.4	82.9	0.264	0.167	0.057	0.165
AME_n consumption	238.4[a]	218.8[b]	195.6[c]	17.849	<0.001	<0.001	0.095
15–17 wk							
Feed consumption	70.6	70.3	69.5	0.223	0.120	0.046	0.710
AME_n consumption	197.9[a]	186.5[b]	164.0[c]	14.445	<0.001	<0.001	<0.001
6–17 wk							
Feed consumption	67.7	68.0	68.1	0.063	0.517	0.194	0.140
AME_n consumption	197.6[a]	180.6[b]	160.6[c]	15.391	<0.001	<0.001	<0.001

[a-c]Means without common superscripts within a row differ significantly ($P < 0.05$).

[1]Values are means of 6 replicates per dietary treatment.

Table 4. Effects of energy-restricted feeding from 6 to 17 wk of age on BW (g) and BW CV (%) of Hyline Brown pullets during sexual maturation.

Items	Control	Energy-restricted feeding (6−17 wk)		SEM	*P*-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
BW (g)							
6 wk	375.9	381.3	377.5	1.953	0.504	0.731	0.266
12 wk	1105.2[a]	1072.6[b]	967.9[c]	4.473	<0.001	<0.001	<0.001
15 wk	1368.8[a]	1330.1[b]	1236.4[c]	4.676	<0.001	<0.001	0.001
16 wk	1413.4[a]	1375.8[b]	1224.6[c]	7.750	<0.001	<0.001	<0.001
17 wk	1474.3[a]	1404.9[b]	1249.8[c]	8.460	<0.001	<0.001	0.001
18 wk	1520.2[a]	1494.4[a]	1399.3[b]	7.271	<0.001	<0.001	0.013
19 wk	1595.0[a]	1539.2[b]	1451.9[c]	5.645	<0.001	<0.001	0.134
20 wk	1692.7[a]	1636.9[b]	1549.1[c]	6.694	<0.001	<0.001	0.216
21 wk	1760.2[a]	1711.5[b]	1612.9[c]	7.261	<0.001	<0.001	0.079
22 wk	1827.1[a]	1853.0[a]	1728.6[b]	7.510	<0.001	<0.001	<0.001
23 wk	1887.5[a]	1898.2[a]	1843.2[b]	6.533	0.001	0.006	0.016
24 wk	1907.6	1919.4	1884.3	6.331	0.071	0.136	0.078
27 wk	1997.1	2009.5	1990.1	6.952	0.512	0.685	0.278
BW CV (%)							
6 wk	10.77	12.38	11.20	0.345	0.140	0.591	0.059
12 wk	7.20	7.22	8.87	0.376	0.110	0.068	0.283
15 wk	6.53	6.55	6.90	0.237	0.796	0.556	0.756
16 wk	7.27	6.47	7.03	0.418	0.776	0.844	0.512
17 wk	6.50	6.77	7.33	0.376	0.713	0.439	0.869
18 wk	7.17	6.77	6.63	0.419	0.894	0.663	0.899
19 wk	7.63[a]	7.27[ab]	6.40[b]	0.244	0.041	0.040	0.605
20 wk	8.45[a]	8.15[a]	6.93[b]	0.254	0.028	0.023	0.320
21 wk	8.73[a]	8.60[a]	7.98[b]	0.245	0.038	0.042	0.652
22 wk	7.68	8.22	8.25	0.283	0.683	0.443	0.694
23 wk	6.62	6.88	8.38	0.340	0.063	0.030	0.349
24 wk	6.27	6.68	7.95	0.298	0.055	0.018	0.449
27 wk	7.25	7.22	7.60	0.324	0.880	0.682	0.778

[a-c]Means without common superscripts within a row differ significantly ($P < 0.05$).

restricted feeding had the lowest progesterone hormone levels at the age of 15 wk and the highest levels at 16 wk ($P < 0.05$).

Sexual Maturity

The age at which the first egg was laid increased linearly, whereas the CV of this age decreased linearly ($P < 0.001$) (Table 9 and Figure 1). The age at 5% and 50% of egg production increased linearly ($P = 0.002$ and 0.001). The number of days and eggs between 5% and 50% egg production declined linearly with the increasing energy restriction levels ($P = 0.046$ and 0.030, respectively).

Productive Performance

The total egg number of laying hens increased linearly ($P = 0.006$), and the CV of individual egg numbers decreased linearly as energy restriction increased ($P < 0.001$) (Figure 2). The egg mass and laying rate

Table 5. Effects of energy-restricted feeding on ADG (g/bird per day), ADFI (g/bird per day), FCR (g/g), and mortality (%) of the pullets from 6 to 24 wk of age.[1]

Items	Control	Energy-restricted feeding (6−17 wk)		SEM	*P*-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
6−17 wk							
ADG	14.27[a]	13.20[b]	11.30[c]	0.436	<0.001	<0.001	0.004
ADFI	67.7	68.0	68.1	0.063	0.517	0.194	0.140
FCR	4.73[c]	5.14[b]	6.03[a]	0.192	<0.001	<0.001	0.001
17−20 wk							
ADG	10.07	11.73	14.57	0.936	0.131	0.054	0.733
ADFI	83.2[b]	84.2[b]	90.7[a]	1.072	0.002	0.001	0.107
FCR	8.52	7.14	6.19	0.508	0.173	0.073	0.83
20−24 wk							
ADG	7.65[c]	10.10[b]	11.90[a]	0.496	<0.001	<0.001	0.587
ADFI	100.5	100.5	103.7	0.815	0.185	0.114	0.338
FCR	13.63[a]	10.07[b]	8.73[b]	0.649	0.001	<0.001	0.250
6−24 wk							
ADG	12.17	12.23	11.93	0.059	0.088	0.097	0.129
ADFI	77.5[b]	77.9[b]	79.8[a]	0.327	0.005	0.002	0.182
FCR	6.38[b]	6.38[b]	6.68[a]	0.044	0.001	0.001	0.026
Mortality	0.56	0.00	3.33	0.668	0.085	0.079	0.149

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

Table 6. Effects of energy-restricted feeding from 6 to 17 wk of age on the sexual organ development of Hyline Brown pullets during sexual maturation.

Items	Week	Control	Energy-restricted feeding (6−17 wk)		SEM	*P*-value		
		2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
Oviduct length (cm)	15	8.10	6.62	6.60	0.432	0.280	0.198	0.343
	17	8.82	9.37	8.62	0.472	0.817	0.871	0.546
	20	27.30[a]	17.45[b]	9.47[c]	2.979	0.038	0.012	0.865
	24	64.20[a]	64.50[a]	60.03[b]	1.439	0.039	0.045	0.247
	28	64.95	65.53	64.60	1.536	0.973	0.931	0.830
	36	57.47	61.10	62.98	1.662	0.411	0.197	0.808
	72	61.88	58.12	59.38	1.225	0.469	0.423	0.354
Oviduct length index (%)	15	6.18	5.15	5.46	0.327	0.440	0.446	0.306
	17	6.28	7.04	7.13	0.364	0.602	0.366	0.677
	20	16.92[a]	11.07[b]	6.36[c]	1.829	0.041	0.016	0.869
	24	33.16	33.85	33.43	0.701	0.932	0.885	0.733
	28	33.71	33.32	33.83	0.653	0.953	0.944	0.766
	36	28.04	30.13	32.46	0.914	0.141	0.052	0.948
	72	30.69	29.00	30.37	0.799	0.681	0.876	0.396
Oviduct weight (g)	15	0.37	0.38	0.33	0.016	0.477	0.373	0.413
	17	0.48	0.43	0.32	0.055	0.479	0.244	0.783
	20	12.35[a]	6.92[b]	1.25[c]	2.205	0.017	0.042	0.979
	24	56.92[a]	56.13[a]	51.60[b]	1.769	0.042	0.024	0.627
	28	55.70[b]	63.80[a]	58.30[ab]	1.365	0.035	0.376	0.015
	36	63.12	59.20	61.20	1.417	0.558	0.598	0.352
	72	73.62[a]	73.08[a]	64.07[b]	1.860	0.047	0.030	0.237
Oviduct index (%)	15	0.28	0.30	0.28	0.012	0.727	0.803	0.455
	17	0.35	0.32	0.26	0.039	0.693	0.406	0.886
	20	7.69[a]	4.33[b]	0.84[c]	1.379	0.025	0.045	0.981
	24	29.37	29.59	28.67	0.940	0.925	0.777	0.789
	28	28.95	32.44	30.69	0.714	0.136	0.303	0.083
	36	30.73	29.18	31.68	0.819	0.482	0.650	0.269
	72	36.46	36.45	32.68	0.948	0.175	0.106	0.339
Ovary stroma weight (g)	15	0.60	0.69	0.63	0.021	0.184	0.724	0.075
	17	0.62[b]	0.74[a]	0.62[b]	0.023	0.039	1.000	0.012
	20	0.83[a]	0.80[a]	0.58[b]	0.069	0.037	0.046	0.550
	24	1.72	1.51	1.62	0.091	0.658	0.665	0.427
	28	1.77	2.06	1.95	0.130	0.681	0.593	0.495
	36	2.03	1.84	1.73	0.086	0.365	0.166	0.843
	72	2.00[a]	1.45[b]	1.52[b]	0.092	0.049	0.022	0.070
Ovary stroma index (%)	15	0.46	0.54	0.52	0.018	0.147	0.201	0.129
	17	0.44[b]	0.56[a]	0.51[ab]	0.018	0.031	0.071	0.024
	20	0.52[a]	0.51[a]	0.39[b]	0.042	0.021	0.047	0.544
	24	0.89	0.79	0.90	0.045	0.599	0.920	0.322
	28	0.92	1.05	1.02	0.064	0.713	0.541	0.590
	36	0.99	0.91	0.89	0.042	0.633	0.381	0.724
	72	1.00[a]	0.72[b]	0.78[ab]	0.050	0.049	0.056	0.096
Small yellow follicles (n)	15	0.17	0.33	0.17	0.101	0.761	0.933	0.470
	17	0.00	0.00	0.17	0.056	0.391	0.240	0.490
	20	6.83[a]	3.33[b]	0.33[c]	1.133	0.035	0.017	0.907
	24	14.17	13.33	13.00	1.219	0.931	0.717	0.928
	28	14.83	14.00	16.17	1.026	0.711	0.618	0.518
	36	13.33	15.67	17.17	1.250	0.478	0.236	0.879
	72	18.33[b]	27.50[a]	20.50[ab]	1.778	0.041	0.589	0.031
Small yellow follicles weight (g)	15	0.01	0.02	0.01	0.004	0.542	0.786	0.291
	17	0.00	0.00	0.01	0.003	0.391	0.240	0.490
	20	0.56	0.37	0.02	0.119	0.170	0.067	0.755
	24	1.86	1.91	1.69	0.184	0.896	0.731	0.757
	28	2.26	2.89	2.84	0.172	0.260	0.175	0.353
	36	1.94	2.19	2.52	0.176	0.429	0.202	0.915
	72	2.20[b]	3.86[a]	2.97[ab]	0.275	0.035	0.197	0.021
Small yellow follicles index (%)	15	0.01	0.01	0.01	0.004	0.592	0.906	0.317
	17	0.00	0.00	0.01	0.002	0.391	0.240	0.490
	20	0.35[a]	0.23[b]	0.01[c]	0.074	0.047	0.039	0.737
	24	0.96	1.00	0.93	0.096	0.966	0.916	0.814
	28	1.18	1.47	1.48	0.085	0.269	0.156	0.434
	36	0.94	1.08	1.31	0.091	0.261	0.110	0.806
	72	1.10	1.93	1.52	0.142	0.050	0.192	0.033

[a-c]Means without common superscripts within a row differ significantly ($P < 0.05$).

Table 7. Effects of energy-restricted feeding from 6 to 17 wk of age on the estradiol level (μg/L) of Hyline Brown laying hens during sexual maturation.

Weeks	Control	Energy-restricted feeding (6–17 wk)		SEM	*P*-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
13 wk	414.86	401.60	436.88	11.591	0.488	0.370	0.435
14 wk	413.20	410.60	435.10	22.472	0.902	0.685	0.852
15 wk	408.56[b]	437.80[b]	519.20[a]	22.944	0.044	0.041	0.868
16 wk	523.44	491.56	502.54	18.281	0.796	0.744	0.563
17 wk	526.00[c]	554.50[b]	597.12[a]	18.739	0.031	0.069	0.906
18 wk	520.18[a]	533.84[a]	399.55[b]	18.993	0.001	0.041	0.041
19 wk	492.32[a]	507.40[a]	385.10[b]	19.262	0.006	0.004	0.110
20 wk	469.92	449.32	517.38	21.543	0.479	0.446	0.446
21 wk	528.24	483.40	482.07	11.468	0.158	0.201	0.201
22 wk	491.46	484.93	508.84	6.281	0.298	0.389	0.389
23 wk	498.94	505.88	489.42	12.253	0.877	0.717	0.727
24 wk	495.28	507.78	525.70	8.009	0.344	0.890	0.890
25 wk	523.10[a]	502.96[ab]	450.58[b]	12.788	0.046	0.861	0.861
26 wk	464.90	465.28	477.34	6.576	0.712	0.441	0.805
27 wk	492.98	478.54	507.36	5.915	0.136	0.181	0.126
28 wk	502.32	527.06	526.90	8.794	0.449	0.344	0.406
30 wk	520.28	532.46	550.52	9.706	0.474	0.233	0.923
32 wk	569.10	571.96	569.72	5.218	0.976	0.997	0.831

[a-c]Means without common superscripts within a row differ significantly ($P < 0.05$).

demonstrated linear increases (P = 0.042 and 0.006) (Table 10). No significant differences were detectable in the average egg weight, feed consumption, feed conversion, AME_n consumption, energy efficiency, or mortality among the treatments ($P > 0.05$).

The rate curve fitting is shown in Figure 3.

$$2,850\,\mathrm{kcal/kg}: \mathrm{y(t)} = 111.4359 \times \mathrm{e}^{-0.0049\times t} / \left[\left(1+\mathrm{e}^{-1.1866\times(t-23.0708)}\right)\right], \mathrm{R}^2 = 0.9883$$

$$2,565\,\mathrm{kcal/kg}: \mathrm{y(t)} = 101.4269 \times \mathrm{e}^{-0.0020\times t} / \left[\left(1+\mathrm{e}^{-1.5534\times(t-23.2951)}\right)\right], \mathrm{R}^2 = 0.9939$$

$$2,280\,\mathrm{kcal/kg}: \mathrm{y(t)} = 105.5410 \times \mathrm{e}^{-0.0025\times t} / \left[\left(1+\mathrm{e}^{-1.6558\times(t-23.9712)}\right)\right], \mathrm{R}^2 = 0.9935$$

The laying rate of hens displayed a linear decrease in the first 2 periods (P = 0.046, at age 18–20 wk; $P <$ 0.001, at age 20–24 wk) but a linear increase in later periods ($P < 0.05$, at age 32–72 wk) (Table 11).

The production of small eggs declined linearly during early laying periods as energy restriction in the growing phase increased, with numbers of 28.37, 27.02, and 20.95 (L, r^2 = 0.821, P = 0.048) (Figure 4). The ad libitum feeding group had fewer large eggs than the energy restriction groups (277.77, 291.12, and 296.52; L, $r^2 = 0.924$, $P = 0.009$).

DISCUSSION

As energy restriction intensified, the BW of layer chicks at age 12 and 15 to 23 wk showed a linear decline. After 7 wk of ad libitum feeding (at age 24 wk), the BW reached that of hens receiving ad libitum feeding.

Table 8. Effects of energy-restricted feeding from 6 to 17 wk of age on the progesterone level (ng/mL) of Hyline Brown laying hens during sexual maturation.

Weeks	Control	Energy-restricted feeding (6–17 wk)		SEM	*P*-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
13 wk	23.62	27.64	30.36	1.356	0.120	0.052	0.516
14 wk	31.56	35.66	35.20	1.245	0.364	0.330	0.301
15 wk	31.38[b]	25.18[c]	39.76[a]	2.054	0.004	0.010	0.011
16 wk	34.54[b]	40.00[a]	25.22[c]	1.808	<0.001	<0.001	0.001
17 wk	25.44	26.20	28.70	1.214	0.553	0.289	0.906
18 wk	29.32	32.58	28.08	1.132	0.261	0.456	0.146
19 wk	30.82	33.10	34.10	1.125	0.489	0.654	0.654
20 wk	38.66	37.56	36.76	1.914	0.931	0.722	0.918
21 wk	42.20	39.78	40.50	0.495	0.117	0.249	0.079
22 wk	42.76	43.88	43.70	0.478	0.625	0.533	0.466
23 wk	45.36	47.86	47.40	0.805	0.396	0.297	0.297
24 wk	43.38[c]	48.30[b]	53.10[a]	1.299	0.002	0.346	0.346
25 wk	55.38	57.96	47.88	2.123	0.128	0.089	0.247
26 wk	55.62	58.08	57.16	0.903	0.567	0.625	0.352
27 wk	61.62[a]	54.60[b]	59.54[a]	1.144	0.029	0.010	0.010
28 wk	58.13	61.90	62.24	1.011	0.277	0.288	0.288
30 wk	63.66	67.86	62.92	1.612	0.433	0.672	0.229
32 wk	68.34	68.78	71.34	1.044	0.482	0.245	0.811

[a-c]Means without common superscripts within a row differ significantly ($P < 0.05$).

Table 9. Effects of energy-restricted feeding from 6 to 17 wk of age on sexual maturity variables of Hyline Brown pullets.[1]

Items	Control	Energy-restricted feeding (6–17 wk)		SEM	*P*-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
Age at 5% egg production (day of age)	140.8^{b}	144.8^{b}	154.3^{a}	1.925	0.005	0.002	0.381
Age at 50% egg production (day of age)	160.2^{b}	160.3^{b}	165.7^{a}	0.802	0.001	0.001	0.040
Age at 90% egg production (day of age)	171.7	173.2	176.2	1.350	0.407	0.195	0.798
5%–50% egg production interval (d)	19.3^{a}	15.5^{ab}	11.3^{b}	1.706	0.026	0.046	0.962
50%–90% egg production interval (d)	11.5	12.8	10.5	1.216	0.757	0.752	0.507
5%–90% egg production interval (d)	30.8	28.3	21.8	2.060	0.188	0.081	0.638
5%–50% egg production egg number (n)	4.3^{a}	2.6^{b}	2.5^{b}	0.352	0.035	0.030	0.239
50%–90% egg production egg number (n)	8.7	9.6	8.1	0.963	0.839	0.817	0.593
5%–90% egg production egg number (n)	13.0	12.2	10.6	1.022	0.650	0.369	0.867

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

Although few studies have investigated the impact of energy restriction in the growing phase on the BW of laying hens, reports have shown that feed-restricted broilers have decreased BW upon completion of the restriction period. Nevertheless, the difference in BW disappears within 1 wk after the feed restriction period in broilers during the second or third week of life (van der Klein et al., 2017). Butzen et al. (2013) found no difference in BW between broilers receiving 80% of the ad libitum intake at the age of 8 to 16 d and those fed with ad libitum at age 42 d. Urdaneta-Rincon and Leeson (2002) observed a decrease in BW of male broilers at age

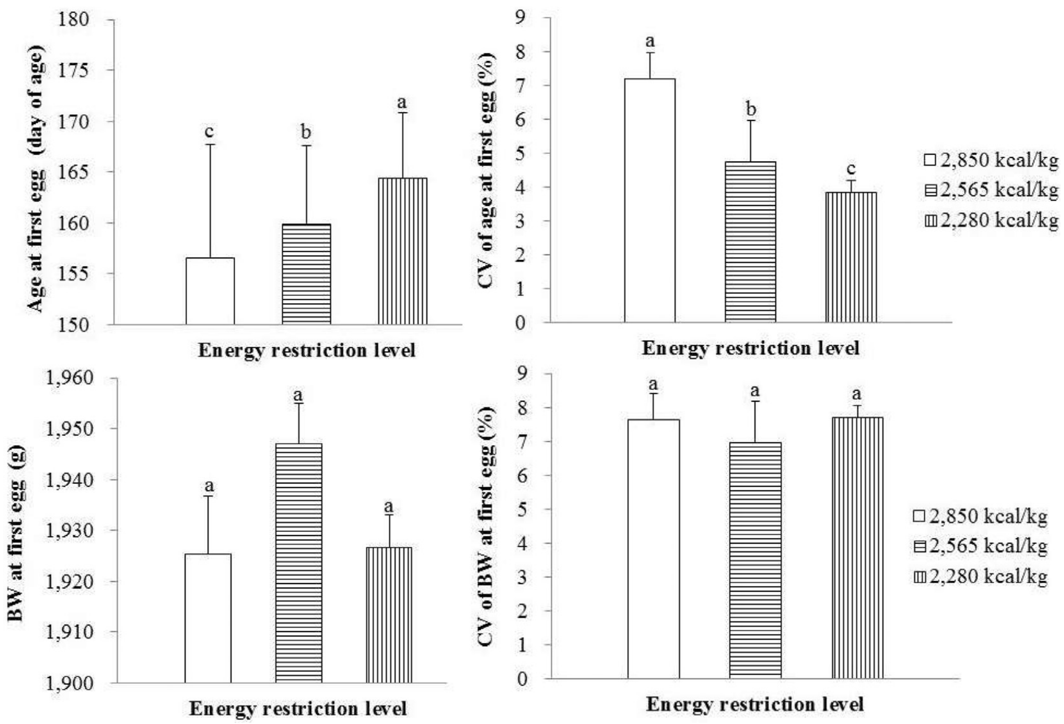

Figure 1. Effects of energy-restricted feeding from 6 to 17 wk of age on age and BW at first egg of Hyline Brown laying hens.

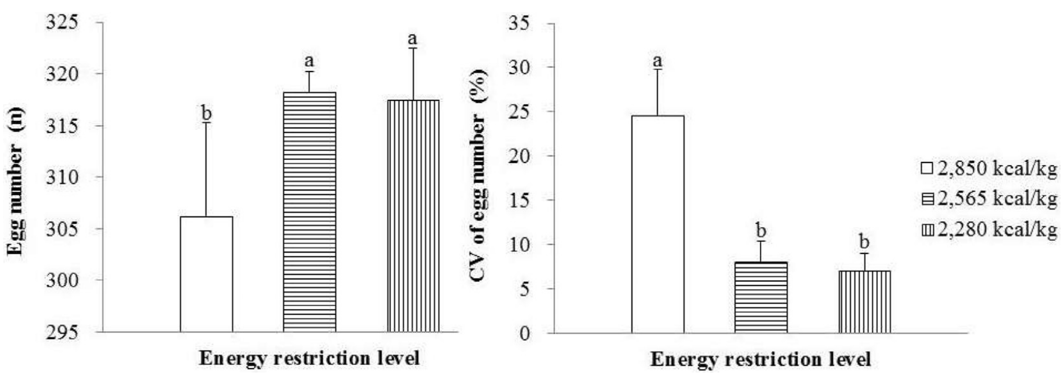

Figure 2. Effects of energy-restricted feeding from 6 to 17 wk of age on the egg number and the CV of individual egg number of Hyline Brown laying hens from 18 to 72 wk of age.

Table 10. Effects of energy-restricted feeding from 6 to 17 wk of age on productive performance of Hyline Brown laying hens from 18 to 72 wk of age.[1]

Items	Control	Energy-restricted feeding (6−17 wk)		SEM	P-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
Laying rate (%)	81.63[b]	84.84[a]	84.66[a]	0.508	0.006	0.006	0.056
Egg weight (g)	61.55	61.07	61.22	0.177	0.552	0.465	0.424
Egg mass (g/d)	50.27[b]	51.80[a]	51.82[a]	0.309	0.042	0.033	0.206
Feed consumption (g/hen per day)	112.3	112.1	113.2	0.336	0.391	0.314	0.354
Feed conversion ratio (kg of feed/ kg of eggs)	2.24	2.16	2.19	0.015	0.114	0.142	0.125
AME_n consumption (kcal/hen per day)	304.5	303.6	307.0	3.946	0.343	0.295	0.306
Energy efficiency (kcal of AME/ g of eggs)	6.07	5.86	5.93	0.177	0.137	0.173	0.134
Mortality (%)	3.33	4.45	5.00	0.886	0.760	0.474	0.889

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

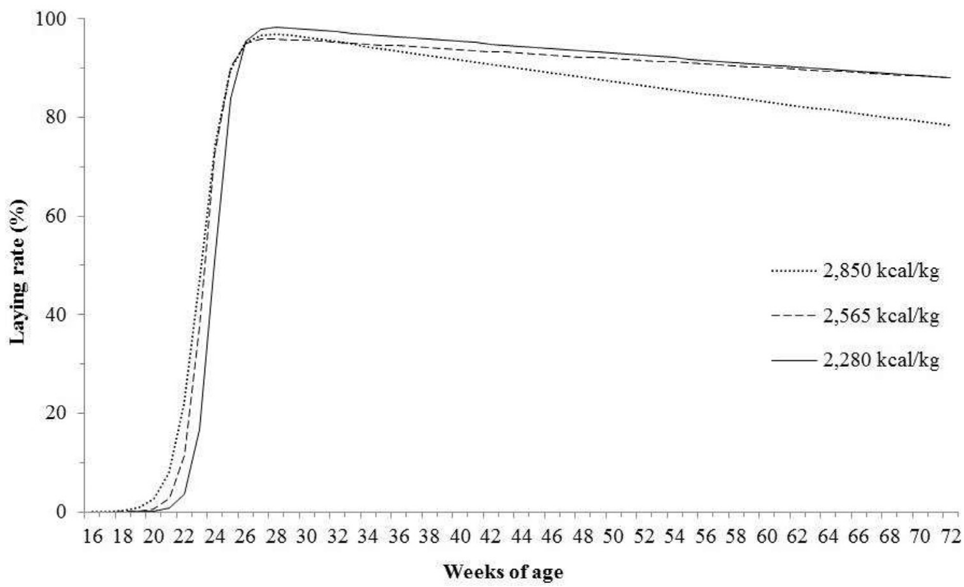

Figure 3. Effects of energy-restricted feeding from 6 to 17 wk of age on laying rate curves of Hyline Brown laying hens.

35 d with feed restriction of 10% at ages 14 to 17, 20, 23, 26, or 29 d, but no differences at 42 or 49 d. There was limited energy intake in the growing phase (age 6−17 wk), resulting in discrepant BWs of pullets between the energy-restricted feeding and ad libitum feeding groups. Despite an increase in the feed intake (nutrient intake) after 6 wk of ad libitum feeding, differences in BW persisted between the 2 groups. Subsequent to ad libitum feeding, the feed intake of laying pullets in the energy-restricted feeding groups rose, triggering rapid compensatory growth and catch-up in the BW at 7 wk postrestriction. Despite the negative impact of energy-restricted feeding on the BW of pullets upon completion of the restriction period and in the following period, their BW was restored to that of the pullets in the ad libitum feeding group subsequent to ad libitum feeding.

Table 11. Effects of energy-restricted feeding from 6 to 17 wk of age on egg production of Hyline Brown laying hens.

Weeks	Control	Energy-restricted feeding (6−17 wk)		SEM	P-value		
	2,850	2,565	2,280		Energy restriction level	Linear	Quadratic
19−20 wk	2.41[a]	0.45[b]	0.00[c]	0.552	0.046	0.038	0.502
21−24 wk	37.94[a]	31.12[a]	17.51[b]	2.540	<0.001	<0.001	0.328
25−28 wk	93.45	94.40	90.94	0.761	0.160	0.173	0.168
29−32 wk	93.34	93.28	96.41	0.692	0.102	0.066	0.254
33−36 wk	93.77[b]	93.87[b]	98.35[a]	0.695	0.002	0.002	0.054
37−40 wk	93.60[b]	95.61[ab]	97.14[a]	0.594	0.039	0.012	0.831
41−44 wk	91.01[b]	95.45[a]	96.70[a]	0.851	0.007	0.003	0.266
45−48 wk	90.57[b]	93.29[ab]	94.54[a]	0.643	0.024	0.008	0.526
49−52 wk	90.67[b]	92.42[ab]	94.18[a]	0.639	0.072	0.024	0.994
53−56 wk	86.88[b]	90.66[a]	91.27[a]	0.727	0.017	0.008	0.224
57−60 wk	82.86[b]	88.86[a]	89.78[a]	1.077	0.008	0.004	0.170
61−64 wk	82.30[b]	90.10[a]	90.28[a]	1.208	0.002	0.002	0.053
65−68 wk	80.00[b]	90.31[a]	90.18[a]	1.408	<0.001	<0.001	0.010
69−72 wk	75.97[b]	86.72[a]	86.53[a]	1.578	0.001	0.001	0.029

[a-c]Means without common superscripts within a row differ significantly ($P < 0.05$).

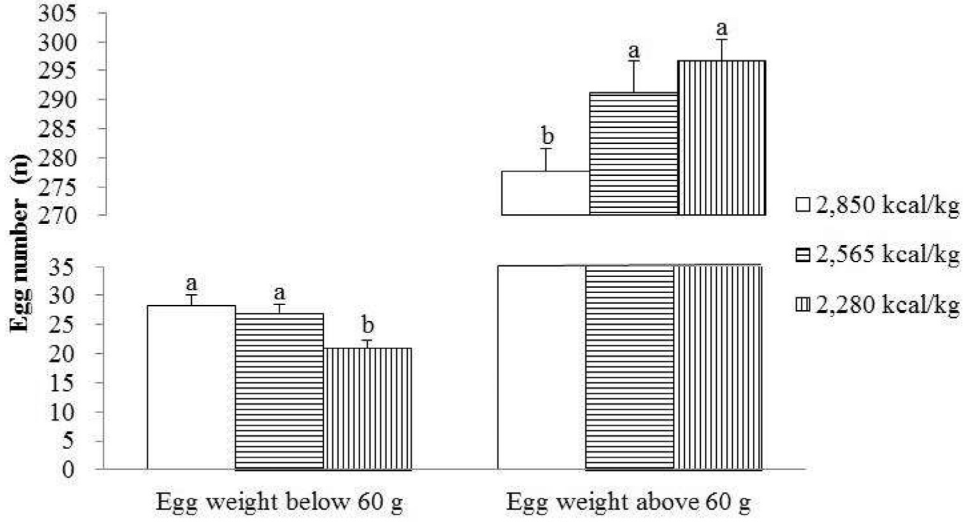

Figure 4. Effects of energy-restricted feeding from 6 to 17 wk of age on egg number (n) of Hyline Brown laying hens.

In addition, energy-restricted feeding led to better BW uniformity, particularly at ages 19, 20, and 21 wk, following the switch to the basal diet. While in broiler breeders, alternative feeding strategies like qualitative diet dilution and skip-a-day management were not found to substantially enhance flock uniformity during the peak period of feed restriction (at age 7−19 wk) compared with the control group. Skip-a-day treatment was more effective than qualitative dilution treatment in improving flock uniformity at age 22 wk (Zuidhof et al., 2015). de Beer and Coon (2007) observed that skip-a-day treatments improved flock uniformity in broiler breeders compared with restricted feeding every day. It is widely believed that the maintenance energy requirement is influenced by the level of feed restriction, age, and ambient temperature (Pishnamazi et al., 2015; Zuidhof et al., 2017). Energy restriction at age 6 to 17 wk may affect the efficiency of nutrition absorption, potentially affecting the maintenance energy requirement and leading to increased BW uniformity. It is desirable to have high flock uniformity among pullets during the onset of sexual maturation, as it can result in a more consistent onset of egg production and greater laying persistency (Bestman et al., 2012).

Energy restriction at age 6 to 17 wk slowed the growth rate of the ovary stroma, small yellow follicles, and oviducts at 20 wk. Feed restriction can regulate the growth rates of the follicles and oviducts in broiler breeders (Hocking, 1993; Bruggeman et al., 1999; Renema et al., 1999). This allows for the delay of sexual organ development and prevents premature sexual maturity (Renema and Robinson, 2004). In our previous study on Rugao layer breeders, energy-restricted feeding at age 8 to 18 wk also resulted in a delay in the development of sexual organs, such as large white follicles, small yellow follicles, preovulatory follicles, oviducts, and ovary stroma at ages 18, 20, and 22 wk (Lu et al., 2021). Body growth was negatively affected by energy-restricted feeding in the growing phase. Subsequent to the energy restriction phase, the pullets experienced rapid body growth, leading to physical maturity and subsequent sexual maturity. After attaining an appropriate BW, the growth of oviducts and ovaries commences (Bédécarrats, 2015). Consequently, pullets in the ad libitum feeding groups achieved physical maturity and developed sexual organs earlier compared with those in the energy-restricted feeding groups. Additionally, there were variations in sexual organ development at age 20 wk but not at 24 or 28 wk, implying that energy-restricted feeding in the growing phase exerts a more pronounced effect on the development of sexual organs than that in the sexual maturity phase, but the effect weakens with age (Lu et al., 2021).

Energy-restricted feeding postpones sexual maturity, including the age at first egg laying and the age at which 5% and 50% of egg production occurs. In White Leghorn chickens reared in the spring, providing two-thirds of the energy in the ad libitum feeding diet from 6 wk to the age at first egg laying resulted in a delay of 3 wk in sexual maturity (Fuller and Chaney, 1974). Similarly, feed restrictions at age 7 to 15 wk and from age 7 wk to the age at first egg laying have been shown to delay the age at first egg laying in Hybro G broiler breeders (Bruggeman et al., 1999). In our previous study on Rugao layer breeders, energy-restricted feeding at age 8 to 18 wk resulted in a delay of 4.2, 8.9, and 5.5 d in the age at first egg laying, age at which 5% of egg production occurred, and age at which 50% of egg production occurred, respectively (Lu et al., 2021). In this trial, hens subjected to 90% energy-restricted feeding showed a delay of 3.2 d in age at first egg laying, while those subjected to 80% energy-restricted feeding showed a delay of 7.9, 13.5, and 5.5 d in age at first egg laying, age at which 5% of egg production occurred, and age at which 50% of egg production occurred, respectively. Furthermore, energy-restricted feeding in the growing phase improved the uniformity of age at first egg laying. Upon completion of energy restriction, BW rapidly increased, and as soon as it reached an appropriate level, sexual organs developed, leading to an acceleration of sexual maturity. Body weight did not differ between the hens subjected to energy-restricted feeding and ad libitum feeding after the ad libitum feeding strategy was adopted for 7 wk (age 168 d). As a result, energy-restricted feeding leads to a delay in the sexual maturity of laying hens.

Restricting energy intake in the growing phase of pullets increases egg production and improves the uniformity of the individual egg number. In broiler breeders, excessive feeding during growing phase can lead to the production of large yellow follicles in multiple hierarchies (Hocking et al., 1989; Katanbaf et al., 1989; Renema et al., 1999), which can be managed by feed restriction programs that increase the number of settable eggs (Hocking et al., 1987; Yu et al., 1992; van der Klein et al., 2020). As reported by Bruggeman et al. (1999), in female Hybro G broiler breeders, restricted energy intake at age 7 to 15 wk, in comparison to ad libitum feeding, boosts the production of total eggs and settable eggs. The current study showed that energy-restricted feeding resulted in a delay in BW and sexual maturity, prolonging the development of the reproductive system and allocating more nutrients toward it. Beyond that, the energy-restricted feeding groups exhibited higher serum estradiol and progesterone concentrations in the later growing phase, which might stimulate the development of sexual organs. Therefore, energy-restricted feeding might improve productive performance throughout the laying phase by facilitating the complete development of the reproductive system. This might raise the developing rate of large yellow follicles and reduced incidence of follicular atresia, internal ovulation, and the membrane production of soft-shelled eggs (Morris and Perry, 2002; Tyler and Gous, 2012). The enhanced flock uniformity in BW and sexual maturity (age at first egg laying) in the energy-restricted groups could also be attributed to initiation of laying within a narrow time range.

In conclusion, our study showed that implementing moderate energy restriction at age 6 to 17 delayed growth, sexual maturity, and sexual organ development during the early laying period of Hyline Brown layer chicks. However, it improved uniformity of BW, age at first egg laying, and individual egg number, and increased egg number per hen, laying rate, average egg mass, and number of settable eggs at age 18 to 72 wk.

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Author Contributions: J. Lu: data curation, writing−original draft preparation. M. Ma: formal analysis. Q. Wang: investigation. Y. F. Li: conceptualization. X. G. Wang: investigation. J. Guo: methodology. T. C. Dou and Y. P. Hu: methodology. Z. Yang: resources. K. H. Wang and L. Qu: supervision, writing−review & editing.

DISCLOSURES

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

SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.psj.2023.102942.

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