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Body composition, gastrointestinal, and reproductive differences between broiler breeders fed using everyday or skip-a-day rearing programs

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ABSTRACT Broiler breeder feed restriction practices have intensified as broiler feed efficiency has been improved. Skip-a-day (**SAD**) rearing regimen has controlled breeder growth, although this practice has become questionable for the modern breeder. We compared everyday (**ED**) and SAD programs and evaluated their impact on pullet growth performance, body composition, gastrointestinal tract development, and reproduction. At d 0, Ross 708 (Aviagen) pullet chicks (n = 1,778) were randomly assigned to 7 floor pens. Three pens were fed using the ED and 4 pens with SAD program through wk 21 using a chain-feeder system. ED and SAD grower diets were formulated to be isonutritious, with the only difference that ED diets had more crude fiber. Pullets (n = 44 per pen) were moved to 16 hen pens by treatment at wk 21 with 3 YP males (Aviagen) in each pen. All birds were fed common laying diets. In addition to BW data, sampled pullets and hens were scanned using dual energy X-ray absorptiometry (**DEXA**) to obtain body bone density and composition. Hen performance and hatchery metrics were recorded through wk 60. ED birds were heavier with similar nutrient intake from wk 10 to 45 ($P \leq 0.013$). Pullet uniformity was unaffected by feeding method ($P \geq 0.443$). SAD pullets had less body fat at wk 19 ($P = 0.034$) compared to ED pullets, likely as a metabolic consequence of intermittent feeding. SAD birds had lower bone density at wk 7, 15, and 19 ($P \leq 0.026$). At 4 wk of age, SAD pullets had less intestinal villi goblet cells compared to ED pullets ($P \leq 0.050$), possibly explained by the effect that feed removal has on cell migration rates. Overall egg-specific gravity ($P = 0.057$) and hatch of fertile % ($P = 0.088$) tended to be higher in eggs from ED hens. Altogether, ED feeding increased young pullet intestinal goblet cells and increased both bone density and body fat at wk 19. ED program improved pullet feed conversion (2.6% less feed) and increased eggshell quality and hatch of fertile.

Key words: feeding regimen, broiler breeder, pullet, gastrointestinal tract, reproduction

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INTRODUCTION

Globally, the economic pressure and protein demand from consumers have encouraged broiler growers to request fast-growing birds from primary breeder companies (Hammerstedt, 1999; Pollock, 1999). The remarkable improvements in broiler chicken growth performance and voracious feed intake posed negative phenotypical effects in both male and female breeder reproduction (Siegel and Dunnington, 1985; Robinson and Wilson, 1996; Kerr et al., 2001; Decuypere et al., 2003). Broiler selection in favor of total carcass lean meat has also reduced the breeder fat deposition (Melnychuk et al., 2004; Carney et al., 2022), which is essential for hens to reach sexual maturity and ovulate (Bornstein et al., 1984).

To adapt to these changes, breeder feed restriction intensified in rearing and moderately during lay to control BW, delay sexual maturity, and improve settable egg production (Fuller et al., 1969; Hocking et al., 1989; Robinson and Wilson, 1996). To mitigate the detrimental effect on BW uniformity during rearing caused by reduced daily feed allowances and competition, skip-a-day (**SAD**) feeding was adopted in the industry. This feeding regime increased the portion size of feed offered to pullets, delayed sexual maturity age, and increased egg size (Harms et al., 1968; Bennett and Leeson, 1989).

Chicken meat consumption, and hence broiler chick demand continues to increase, while hatchability and egg production has declined over the last few years (Agri Stats, 2021; USDA, 2022). Also, pullet mortality has

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increased 1% in the last 5 yr (Agri Stats, 2021), pressuring the industry to question whether modern feed restriction exacerbates metabolic diseases (Clark et al., 2019), mortality, and reproductive issues. As a result, these complications have encouraged the search for nutritional or management strategies that can ameliorate the detrimental effect of intensive feed restriction programs such as SAD. There is a lack of updated research that indicates whether SAD program is entirely beneficial for pullet growth and subsequent reproduction under commercial U.S. housing and feeding systems. To avoid poor BW uniformity and performance, the industry in the United States has been reluctant to transition to an everyday (**ED**) regimen. Recent studies comparing these 2 regimes have used a common pullet diet (de Beer and Coon, 2007; Sweeney et al., 2022), although in practice, adopting a daily feeding program in long pullet houses (90−150 m) requires voluminous diets that allow proper feed distribution and prolong feeding time (Wilson, 2003; Burnham, 2021). High fiber diets are considered the best option for daily feeding to reduce feeding frustration, promote satiety, and slow feed passage in the proximal gastrointestinal tract (de Jong et al., 2005; Mateos et al., 2012).

Several decades ago, researchers demonstrated that SAD was meaningful to control BW uniformity (Luckham et al., 1963; Fuller et al., 1969; Wilson et al., 1983), although this regime can have negative consequences in modern breeders. SAD pullets are more stressed and maintain a negative energy balance on days without feed compared to pullets fed daily (Bennett et al., 1990; de Beer et al., 2008). Also, ED feeding using broadcasting systems has enhanced the pullet innate immune response against *E. coli* and *S. enteritidis* (Montiel, 2016). Feed restriction and removal induce gastrointestinal tract (**GIT**) sloughing, impairing its development (Holt et al., 1986; Shamoto and Yamauchi, 2000) and affects bone growth in growing chickens (Hudson et al., 1999; Bruno et al., 2000, 2007), all crucial characteristics for growing pullets, hen eggshell formation, and overall reproduction (Dacke et al., 1993). Also, most recent studies have demonstrated that ED feeding does not compromise BW uniformity, while ED feeding stimulates proper age at sexual maturity, and improves egg production (de Beer and Coon, 2007; Montiel, 2016; Sweeney et al., 2022). Altogether, intensive feed restriction regimens such as SAD can have serious consequences in breeder growth and reproduction, and these outcomes could partially explain the current issues that breeder operations face. To provide the industry more information regarding the physiological and reproductive differences between pullets fed under these regimens, the objectives of this study were to compare the effect of pullet ED program with a customized diet for this regimen, and SAD programs on broiler breeder: 1) growth performance, 2) body composition, 3) skeletal bone density, 4) GIT development, and 5) overall reproductive performance.

MATERIALS AND METHODS

All experimental procedures used in this study were approved by The University of Georgia Institutional Animal Care and Use Committee (AUP#: A2020 03-008-A2).

Rearing

At 1 d of age, Ross 708 (Aviagen Group, Huntsville, AL) broiler breeder pullets (n = 1,778) were obtained from a primary breeder hatchery. Pullet chicks were randomly distributed to 7 pens (7.3 × 4.6 m^2) at a density of 7.5 birds per m^2 (n = 254 birds per pen). The rearing facility was light tight, with forced air heat, and evaporative cooling. Temperature was reduced from 31°C to 21°C during the first 15 d according to bird's comfort and then maintained close to 21°C through wk 21. To mimic common U.S. feeding equipment, pullets were fed using chain-feeder systems (Big Dutchman Inc., Holland, MI) providing 12 cm of linear trough space per bird, and water was provided free choice by a nipple drinker. A commercial vaccination program was followed through wk 21. All aspects of rearing were maintained as close to industry standards as possible in a research facility. Pullet chicks were exposed to 24 h of light the first day, switched to 23 h of daylight for 3 d and then reduced to 8 h of daylight through wk 21 (9 Lux always). All birds were wing-banded at wk 8.

Feeding Program Treatments

All birds were fed ad libitum a common starter during the first 3 wk (Table 1). At wk 4, pens were assigned their respective feeding program, but also a respective diet formulation for each program. A 2-stage grower diet program was fed: Grower I from wk 4 to 10, and Grower II from wk 11 to 22 (Table 1). ED and SAD grower diets were formulated to be isocaloric, isonitrogenous (including amino acids) to the best of our efforts using common industry ingredients. The only difference being that ED diets provided more crude fiber from whole oats and soy hulls to increase volume. Three pens were fed using the ED and 4 pens with the SAD program through wk 21. Feeding time was 7:00 am during the rearing period. SAD-fed birds were given twice the amount of feed compared to ED-fed birds on the feed day. For example, if ED pullets were given 40 g of feed per day, SAD pullets would be fed 80 g every other day. Both feeding methods provided the same feed amount per bird over a 2-day period, and feed allowance was equally adjusted every wk based on BW means obtained from BAT1 electronic hanging scales (VEIT Electronics, Moravany, Czech Republic).

Body Weights and Mortality

All birds from all pens were weighed individually during wk 5, 10, 15, and 20 on a day off feed for the SAD

Table 1. Broiler breeder pullet rearing diet composition.

Ingredient	Starter[1] %	Grower I[2] SAD %	Grower I[2] ED %	Grower II[3] SAD %	Grower II[3] ED %
Ground corn	58.73	57.30	55.59	59.07	53.46
Soybean meal	24.23	15.30	15.99	13.32	13.28
Oats, whole	-	-	6.00	-	8.00
Soy hulls	-	-	2.02	-	1.59
Wheat middlings	11.00	22.00	15.03	22.52	18.00
Soybean oil, crude	1.00	1.00	1.00	0.70	1.31
Limestone	1.51	1.48	1.43	1.57	1.53
Mono-dicalcium phosphate	2.24	1.87	1.94	1.69	1.72
L-lysine HCL	0.12	0.05	0.03	0.10	0.09
DL-methionine	0.28	0.15	0.15	0.16	0.16
L-threonine	0.12	0.10	0.10	0.11	0.12
Sodium chloride	0.32	0.31	0.32	0.29	0.29
Sodium sesquicarbonate	0.16	0.13	0.11	0.16	0.15
Choline chloride 60%	0.11	0.13	0.12	0.14	0.13
Vitamin premix[4]	0.05	0.05	0.05	0.05	0.05
Mineral premix[5]	0.08	0.08	0.08	0.08	0.08
Sand	0.05	0.05	0.05	0.05	0.05
Total	100.00	100.00	100.00	100.00	100.00
Calculated nutrients					
ME, Mcal/kg	2.852	2.787	2.787	2.785	2.785
Crude protein, %	18.10	15.28	15.29	14.63	14.60
Ether extract, %	2.72	2.99	2.98	3.07	3.06
Crude fiber, %	3.21	3.94	4.53	3.96	4.75
Ca, %	1.05	0.95	0.95	0.95	0.95
Av. P, %	0.47	0.43	0.43	0.40	0.40
Dig. lysine, %	0.82	0.60	0.60	0.60	0.60
Dig, Met + Cys, %	0.71	0.54	0.54	0.53	0.53
Dig. methionine, %	0.49	0.34	0.34	0.34	0.34
Dig. threonine, %	0.59	0.49	0.49	0.48	0.48
Dig. tryptophan, %	0.17	0.14	0.14	0.13	0.13
Dig. isoleucine, %	0.58	0.47	0.48	0.43	0.44
Dig. valine, %	0.62	0.52	0.53	0.50	0.51
Dig. leucine, %	1.27	1.09	1.08	1.05	1.03
Dig. arginine, %	1.02	0.84	0.85	0.79	0.80
Dig. histidine, %	0.36	0.31	0.30	0.30	0.29
Dig. phenylalanine, %	0.70	0.57	0.58	0.54	0.55

[1]Crumbled starter feed was fed ad libitum from wk 1 to 3.
[2]Mash Grower I diets were fed after wk 3 until wk 10 of age.
[3]Mash Grower II diets were fed after wk 10 until wk 22 of age.
[4]Provided per kg of feed: vitamin A, 13,228 IU; vitamin D3, 3,505 IU; vitamin E, 100; vitamin B12, 0.004 mg; menadione, 6.6 mg; riboflavin, 11 mg; pantothenic acid, 28.6 mg; niacin, 55 mg; folic acid, 4.4 mg; pyridoxine, 6.6 mg; thiamine 2.2 mg; biotin, 0.3 mg.
[5]Provided per kg of feed: Mg, 21 mg as Mg oxide; Mn, 107 mg as Mn sulfate; Zn, 86 mg as Zn sulfate; Fe, 21 mg as ferrous sulfate; Cu 3 mg as Cu sulfate; I, 0.8 mg as Ca iodate; Se, 0.3 mg as sodium selenite.

birds, and ED pullets were weighed prior to feeding. These data were used to determine BW uniformity expressed as coefficient of variation (%). Mortality was recorded daily by pen through rearing.

Pullet Body Scans

To determine the effect of feeding program on pullet body composition and bone density, pullets ($n = 12$ per treatment) were scanned using dual X-ray absorptiometry (**DEXA**) Lunar Prodigy scanner (GE Healthcare, Chicago, IL) during wk 3, 7, 11, 15, and 19, as described in previous experiments (Chen et al., 2022). Sampled pullets were randomly selected from the pens within a ±1 standard deviation from the pen mean BW. Those randomly selected that were outside the desired BW range were returned to the pen. At all timepoints, pullets were caught 7 h postfeeding time (2:00 pm) on the day off from feed for the SAD pens and to allow ED pullets to have less feed in the gastrointestinal tract. Pullets were euthanized via hypoxia achieved through exposing the birds to high concentrations of CO_2 gas before scanning. Body composition was expressed as relative (% of BW) and as absolute weight (g per bird).

Gastrointestinal Tract Sampling

To assess the effect of feeding program on pullet GIT organ and histological morphology, during wk 4, 10, 16, and 22 birds ($n = 24$ per treatment at each wk) were chosen within ±1 standard deviations from their pen mean BW and euthanized via electrical stunning and cervical dislocation. Birds were caught prior to feeding time at 7:00 am on a feed day for ED and SAD pullets. Empty crop, proventriculus, gizzard, and whole liver were removed and weighed. Empty midsections of the ileum, jejunum, and duodenum were collected and put in containers with 10% buffered formalin as described by Sweeney et al. (2022). Formalin-fixed intestine samples were then sent to a histopathology laboratory at the University of Georgia Poultry Disease Research & Center (Athens, GA) for paraffin embedding, sectioning, Alcian Blue staining, and counterstained with fast nuclear-red. All intestine sections on glass slides were imaged using a BZ-X810 microscope (Keyence, Osaka, Japan) and analyzed using ImageJ software (National Institute of Health, Brethesda, MD). The length of villi and crypt depth of 3 representative villus per bird's tissue were measured. Additionally, all goblet cells stained with Alcian Blue were manually enumerated using the multipointer feature of ImageJ and expressed as goblet cells per villus.

Laying Period and Reproductive Performance

Bird Husbandry After the rearing period, 21-wk-old pullets ($n = 704$ pullets total) were designated to a laying pen ($n = 44$ birds per pen; 2.4×3.6 m^2) with each pen having similar mean treatment BW and uniformity. Eight pens contained pullets reared under SAD and another 8 with pullets reared under ED. Two thirds of the floor space was covered by slats, and the remaining third of the pen was covered with pine shavings. A 6-hole nest section was placed on the slats of each pen. When pullets were moved to hen pens (21 wk of age), photoperiod was changed directly from 8 to 15 h of light per day. At wk 23, Yield Plus males (Aviagen; 3,352 ± 190 g of BW) of the same age and grown separately were included in each hen pen. Males were replaced due to mortality or lameness with males of the same age through 52 wk of age. To mimic industry practices, 1 Yield Plus spike male (3,943 ± 240 g of BW) of 23 wk of age was added to each pen when hens were 52 wk old, totaling 4 males per pen (3 original + 1 spike male). Hens were fed using Chore-time (Chore-time equipment, Milford, IN) pan feeders ($n = 4$ per pen) with an

exclusion grill to prevent males from accessing the hen feeder. Pan feeders were filled with feed ED according to daily allowance and hand-lowered every morning at 6:30 am. Males were fed from plastic (4 hole) suspended feeders (Fortex-Fortiflex, San Juan, PR) over the shavings area. All birds had free access to water with a nipple drinker line. A sample of hens and roosters were individually hand-weighed weekly ($n = 2$ whole pens per treatment) to adjust feed allowance based on BW gain, and in the case of hens, egg production. Feed was equally adjusted through lay for the hens (80−157 g per bird) and roosters (91−139 g per male). During the laying period, all birds were fed a common prelay diet from wk 22 to 25 (14.1% CP, 2,825 kcal/kg, and 1.5% Ca), switched to a breeder I diet at wk 26 wk (14.1% CP, 2,785 kcal/kg, and 3.2% Ca), and then a breeder II diet from 46 to 60 wk (14.0% CP, 2,785 kcal/kg, and 3.3% Ca). All diets were corn and soybean meal-based and fed mash-form.

Egg Production and Egg Weight

Eggs were collected 4 to 5 times a day, recorded, and graded by pen. The egg production per pen was expressed as weekly egg production (%). A flat of settable eggs per pen was weighed weekly to determine average egg weight.

Eggshell Quality

Shell quality was evaluated by the specific gravity floatation method ($n = 1$ d worth of settable eggs per pen) during wk 30, 34, 38, 42, 46, 50, 54, and 58. Eggs collected for this procedure were stored in the same room as the salinity tanks for approximately 15 h to allow the eggs to come to the same temperature as the solutions. Eggs sorted by pen were floated in water tanks with salinity levels ranging from 1.060 to 1.095 g/cm^3. A weighted mean shell quality score was determined by pen. This analysis was performed on 2 separate days after wk 50 to increase the sample size evaluated.

Incubation

Settable eggs ($n = 1{,}620$ per time point) were incubated 9 times by pen during the laying period during wk 29, 33, 37, 41, 45, 49, 54, 57, and 60. Eggs were incubated in Natureform incubators (Natureform Inc., Jacksonville, FL) at 37.5°C (53% of relative humidity) and rotated 45° every 2 h during the first 18 d of the 21-day incubation period. To determine fertility and early embryo mortality, eggs were candled 11 d after being set, and transferred to a hatcher at incubation d 18 with temperature set to 37°C for the remaining 3 d. Hatchability and embryo analysis was performed at every hatch.

Hen Body Scans

During wk 25, 35, 45, and 55 hens ($n = 1$ per pen at wk 25, 35, and 45; $n = 2$ per pen during wk 55) were selected using the same procedure as the pullets and scanned using DEXA.

Statistical Analysis

Data were analyzed using a generalized linear model (**GLM**) for analysis of variance using Statistical Analysis System (**SAS**) version 9.4. Means were declared different when $P \leq 0.05$. Tendencies were declared when $P > 0.05$ and ≤ 0.10 (Desbiens, 2003). All data were analyzed by timepoint, and hen reproductive performance and hatchery data were analyzed by periods: early lay (25−45 wk), late lay (46−60 wk), and overall (25−60 wk). Age effect P value was calculated for DEXA analysis to examine the body composition changes as breeders age.

RESULTS

Pullet Growth

Results from Table 2 indicate that ED-fed pullets were 4.5, 3.5, and 4.4% heavier than SAD pullets during wk 10, 15, and 20, respectively ($P < 0.001$). Uniformity (CV%) was not impacted by feeding program through rearing ($P \geq 0.443$). Pullet mortality was not affected by

Table 2. Effect of rearing feed restriction program on broiler breeder pullet BW, uniformity, mortality, and feed conversion.

	Feeding program[3]			
Item[1]	SAD	ED	SE	*P* value
BW, g by wk				
5	529	524	3	0.178
10	892[b]	932[a]	6	<0.001
15	1,382[b]	1,430[a]	9	<0.001
20	1,877[b]	1,959[a]	13	<0.001
Uniformity, CV % of BW by wk				
5	13.9	13.8	0.4	0.826
10	15.0	16.5	1.3	0.443
15	15.2	16.3	1.1	0.451
20	15.5	16.0	1.0	0.712
Mortality, by wk period				
≤5[1]	-	-	-	-
5−10	0.3	0.5	0.2	0.399
11−15	0.7	0.5	0.3	0.733
16−21	0.8	0.5	0.2	0.286
Cumulative	1.77	1.58	0.5	0.773
Feed conversion, kg per live pullet[2]	6.997[a]	6.853[b]	0.02	0.001

[1]Mortality data and feed consumption from d 0 to 5 wk of age were not used in the analysis due to pullet mortality caused by bacterial infection coming from the hatchery and confirmed by University of Georgia Poultry Disease and Research Center, Athens, GA.

[2]Feed conversion, kg per live pullet = total feed fed to pullet pen/live pen pullets at wk 21.

[3]Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen, and ED = everyday feeding regimen.

[a,b]Means with different superscripts within rows denote significant differences ($P \leq 0.05$).

feeding program ($P \geq 0.286$), although the feed conversion per live pullet improved in ED pens (6.853 vs. 6.997 kg per pullet; $P = 0.001$), indicating that less feed (2.6%) was utilized per live pullet through the rearing period.

Body Composition and Bone Density

Figure 1A and B displays the effect of pullet feeding regimen on breeder relative lean muscle and fat %, respectively, as measured by DEXA. Regardless of treatment, pullet body composition prior to wk 25 was 89 to 94% lean muscle (age effect: $P < 0.001$; Figure 1A), whereas relative fat % doubled from wk 25 to 35 (age effect: $P < 0.001$; Figure 1B), as relative lean muscle % decreased. The pullet feeding program did not influence relative lean muscle or fat % during rearing (wk 3−19) or lay (wk 25−55; $P \geq 0.218$). Figure 1C and D shows the effect of feeding regimen on breeder lean muscle and fat contents expressed as g per bird, respectively. SAD pullets possessed less lean muscle mass during wk 11 to 19 ($P \leq 0.048$), with a similar tendency detected at wk 25 ($P = 0.084$; Figure 1C). Total body fat content in ED pullets was higher at wk 19 (120 vs. 89 g of fat per bird; $P = 0.034$; Figure 1D).

Figure 2A to C shows that regardless of treatment, age had an overall positive relationship on breeder relative bone %, absolute bone mineral weights, and bone mineral density, respectively (age effect: $P < 0.001$). Relative bone mineral % was higher in ED pullets at wk 7 ($P = 0.012$) as shown in Figure 2A. Higher bone mineral content (g per bird) was detected in pullets fed ED at wk 7, 15, and 19 ($P \leq 0.027$; Figure 2B). Figure 2C

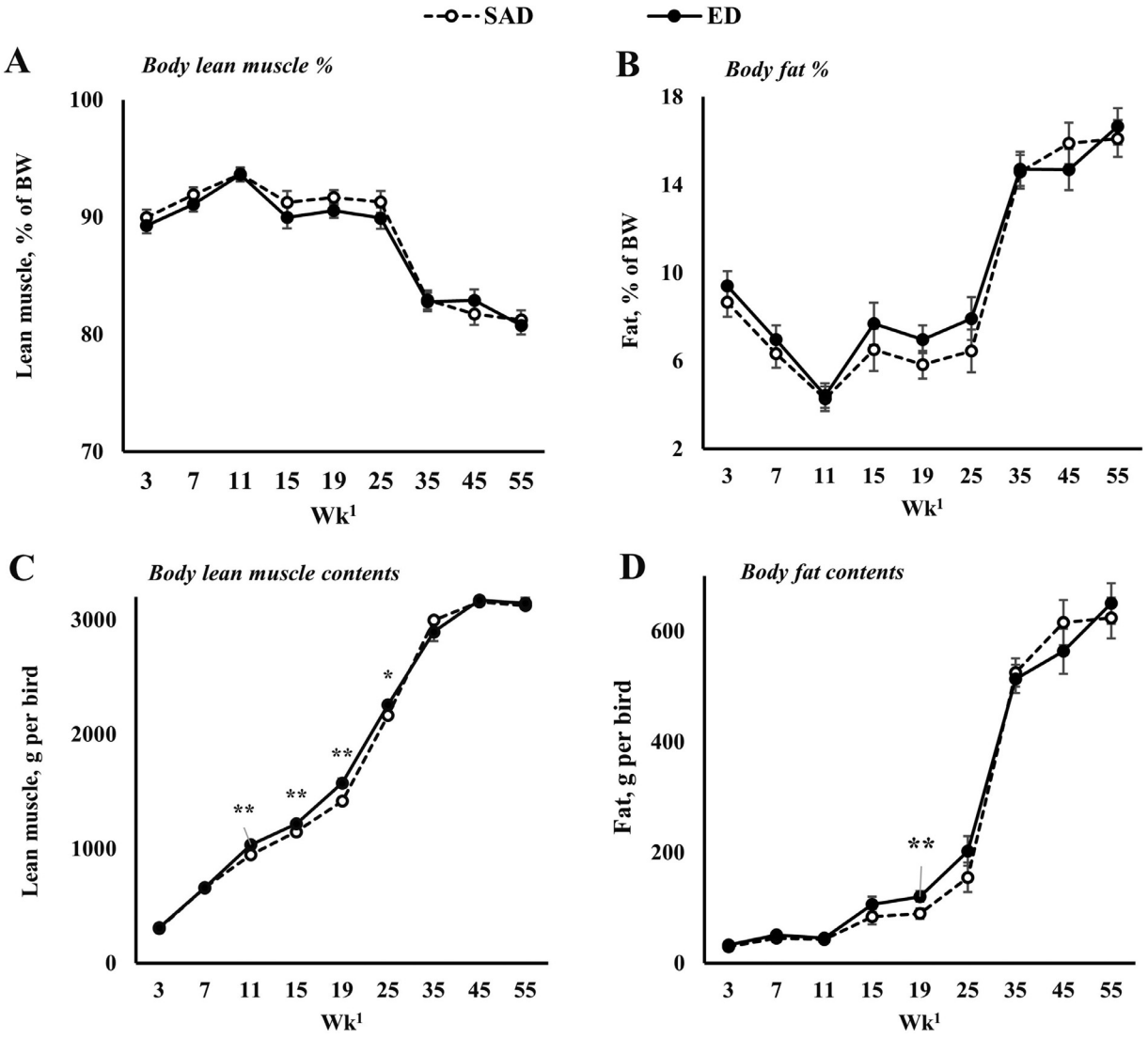

Figure 1. Effect of rearing feed restriction program on breeder relative lean muscle % (A), relative fat % (B), and absolute lean muscle and fat weights (g per bird; C and D, respectively). Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen; and ED = everyday feeding regimen. All birds were fed daily through lay starting at wk 21. A total of $n = 12$ pullets per treatment were sampled during rearing using DEXA scanner; $n = 8$ per hens per treatment at wk 25, 35, and 45; $n = 16$ hens per treatment sampled at wk 55. [1]Age effect $P < 0.001$ for all figures. Significant differences between treatments at each timepoint (**) were declared when $P \leq 0.05$, and tendencies (*) declared when $0.05 > P \leq 0.10$. Error bars represent ± SE at each timepoint for treatment effect. Body lean muscle and fat % was not affected by rearing regimen ($P \geq 0.218$). Skip-a-day pullets possessed less lean muscle mass during wk 11 to 19 ($P \leq 0.048$), with a similar tendency detected at wk 25 (C; $P = 0.084$). Total body fat contents in ED pullets were higher at wk 19 compared to SAD pullets (120 vs. 89 g per bird; $P = 0.034$).

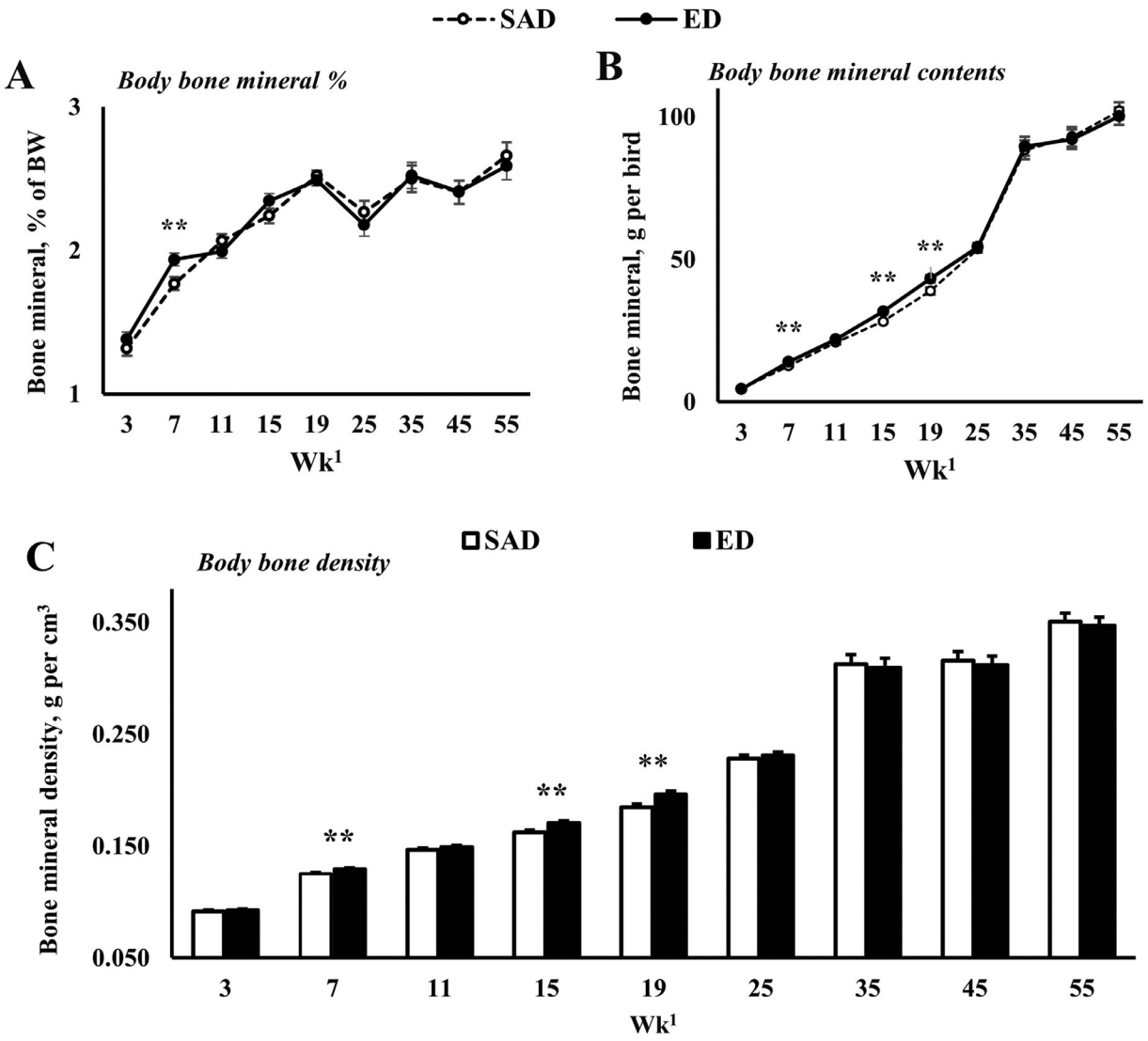

Figure 2. Effect of rearing feed restriction program on breeder relative bone mineral % (A), absolute bone mineral weight (g per bird; B), and bone density (C). Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen; and ED = everyday feeding regimen. All birds were fed daily through lay starting at wk 21. A total of $n = 12$ pullets per treatment were sampled during rearing using DEXA scanner; $n = 8$ per hens per treatment at wk 25, 35, and 45; $n = 16$ hens per treatment sampled at wk 55. [1]Age effect $P < 0.001$ for all figures. Significant differences between treatments at each timepoint (**) were declared when $P \leq 0.05$. Error bars represent ± SE at each timepoint for treatment effect. Pullets fed under ED had more relative mineral contents at wk 7 ($P = 0.012$; A), and body mineral contents at wk 7, 15, and 19 compared to SAD birds ($P \leq 0.027$; B). Denser bones were detected in pullets fed under ED program at wk 7, 15, and 19 ($P \leq 0.026$; C).

shows that pullets fed under ED regime had increased bone mineral density at wk 7, 15, and 19 compared to SAD pullets (Figure 2C; $P \leq 0.026$). The bone mineral density was not affected during the laying period by rearing feed regime (wk 25−55; $P \geq 0.522$).

Gastrointestinal Tract

Organ Weights Table 3 shows the relative organ weights (% of pullet BW) during wk 4, 10, 16, 21. Heavier relative crop weights were detected in SAD pullets at all timepoints ($P \leq 0.003$), as well as larger relative proventriculus during wk 10, 16, and 21 ($P \leq 0.001$). Relative gizzard weights were larger in SAD pullets, but only at the end of the rearing period (wk 21; $P < 0.001$). Like other organs, relative liver weight of SAD pullets tended to be higher at wk 10 ($P = 0.071$) and were significantly heavier at wk 16 and 21 ($P < 0.001$).

Histology Measurements Histological results in Table 4 show that ED pullets had more villi goblet cell populations in the ileum, jejunum, and duodenum at wk 4 ($P \leq 0.050$). Also, ED pullets had increased duodenal villi goblet cells at wk 10 ($P = 0.015$). In contrast, jejunal goblet cell populations tended to be higher in SAD pullets at wk 10 ($P = 0.082$). No changes in goblet cell populations were observed at wk 16 or 21 ($P \geq 0.346$). Jejunal villi tended to be shorter in SAD pullets at wk 16 ($P = 0.097$), and deeper ileal crypts were detected in ED-fed pullets at wk 4 and 10 ($P \leq 0.039$). Daily-fed pullets tended to have higher duodenal villus-to-crypt ratio at wk 4 compared to SAD pullets ($P = 0.080$), but an opposite tendency was detected in the ileum at wk 10 ($P = 0.099$).

Table 3. Effect of rearing feed restriction program on broiler breeder pullet relative gastrointestinal organ weights (% of BW) at ages 4, 10, 16, and 21 wk.

Item[1]	Feeding program[2] SAD	ED	SE	*P* value
WK 4				
Crop, % of BW	0.83[a]	0.75[b]	0.02	0.003
Proventriculus, % of BW	0.56	0.59	0.01	0.101
Gizzard, % of BW	4.21	4.39	0.09	0.149
Liver, % of BW	1.98	1.96	0.03	0.750
Wk 10				
Crop, % of BW	0.70[a]	0.49[b]	0.01	<0.001
Proventriculus, % of BW	0.43[a]	0.36[b]	0.01	<0.001
Gizzard, % of BW	3.17	3.16	0.09	0.954
Liver, % of BW	1.50[x]	1.39[y]	0.04	0.071
Wk 16				
Crop, % of BW	0.63[a]	0.39[b]	0.01	<0.001
Proventriculus, % of BW	0.34[a]	0.28[b]	0.01	<0.001
Gizzard, % of BW	2.68	2.52	0.09	0.182
Liver, % of BW	1.47[a]	1.25[b]	0.03	<0.001
Wk 21				
Crop, % of BW	0.49[a]	0.35[b]	0.01	<0.001
Proventriculus, % of BW	0.26[a]	0.23[b]	0.12	<0.001
Gizzard, % of BW	2.18[a]	1.73[b]	0.06	<0.001
Liver, % of BW	1.25[a]	1.17[b]	0.03	0.036

[1]Pullets ($n = 24$ per treatment at each age) were euthanized and sampled during wk 4, 10, 16, and 21. All empty organ weights are relative to BW (%).

[2]Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen; and ED = everyday feeding regimen.

[a,b]Means with different superscripts within rows denote significant differences ($P \leq 0.05$).

[x,y]Means with different superscripts within rows denote tendencies ($0.05 > P \leq 0.10$).

Reproductive Performance

Table 5 displays the reproductive performance of hens reared under ED or SAD. Egg production did not differ between treatment groups ($P \geq 0.247$). Hens reared under ED were 61 g heavier during early lay (25–45 wk; $P = 0.013$), and on average throughout lay ($P = 0.037$). Hens fed daily as pullets remained more uniform during lay ($P = 0.001$) and laid heavier eggs during early lay ($P = 0.036$) and overall ($P = 0.015$) compared to SAD hens. Egg-specific gravity measures indicated that ED hens had higher eggshell quality during late lay (wk 46–60; $P = 0.006$), and on average specific gravity tended to be higher in ED eggs compared to those laid by SAD hens ($P = 0.057$). Hen age at sexual maturity, eggs and chicks per hen housed, feed conversion, and mortality were not influenced by rearing feeding program ($P > 0.10$).

Table 6 shows the effect of rearing program on hatchability and incubation parameters of eggs laid by both hen groups. Fertility and hatchability were not influenced by rearing program ($P > 0.10$), although overall hatch of fertile % tended to be higher when incubating eggs from ED hens compared to SAD hens ($P = 0.088$), since late embryonic dead % tended to be lower in ED eggs when incubated during late lay and overall ($P \leq 0.082$). Overall contaminated eggs ($P = 0.020$) and dead pips were more prevalent ($P = 0.036$) when eggs were obtained from SAD hens compared to those from ED hens.

DISCUSSION

Pullet Growth and Body Composition

In our study, ED-fed pullets were heavier at most times during rearing and early lay, and this agrees with recent studies where the feed allocation was the same on a 2-day basis for both treatments (de Beer and Coon, 2007; Sweeney et al., 2022). Sweeney et al. (2022) found

Table 4. Effect of rearing feed restriction program on broiler breeder pullet intestinal goblet cell populations, villus length, crypt depth, and villus-to-crypt ratio.

Variable[1], by wk	Ileum SAD	ED	SE	*P* value	Jejunum SAD	ED	SE	*P* value	Duodenum SAD	ED	SE	*P* value
Goblet cells per villus												
4	257[b]	317[a]	17	0.014	293[b]	343[a]	18	0.050	286[b]	364[a]	23	0.022
10	348	303	26	0.221	402[x]	335[y]	27	0.082	254[b]	336[a]	24	0.015
16	340	372	24	0.348	383	348	25	0.346	326	345	23	0.551
22	346	341	23	0.864	324	315	17	0.740	274	264	17	0.677
Villus length, μm												
4	819	855	28	0.358	1,062	1,120	33	0.212	1,604	1,722	77	0.272
10	905	959	26	0.137	1,274	1,273	37	0.993	1,702	1,784	70	0.401
16	918	955	42	0.538	1,229[y]	1,351[x]	52	0.097	1,918	1,890	47	0.663
22	952	993	46	0.506	1,383	1,395	69	0.893	1,798	1,739	69	0.524
Crypt depth, μm												
4	96[b]	126[a]	8	0.012	120	126	9	0.640	144	130	7	0.169
10	84[b]	100[a]	6	0.039	86	100	6	0.101	100	111	8	0.331
16	99	92	6	0.413	93	92	5	0.965	122	129	7	0.474
22	91	101	7	0.323	98	93	9	0.616	103	109	8	0.566
Villus:crypt ratio												
4	8.8	7.6	0.5	0.110	9.1	10.1	0.6	0.248	11.7[y]	13.9[x]	0.9	0.080
10	11.5[x]	10.1[y]	0.6	0.099	15.8	14.1	1.1	0.241	19.2	17.0	1.3	0.220
16	9.9	11.0	0.7	0.247	14.0	16.0	1.2	0.251	17.2	15.5	1.1	0.258
22	11.4	10.5	0.7	0.340	15.9	16.2	1.1	0.844	19.0	17.5	1.4	0.429

[1]Pullets were sampled at wk 4, 10, 16, and 22 ($n = 24$ per treatment per wk). All tissue slides were processed and stained with Alcian Blue for staining goblet cells and fast nuclear-red as a counter stain. Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen; and ED = everyday feeding regimen.

[a,b]Means with different superscripts within rows denote significant differences ($P \leq 0.05$).

[x,y]Means with different superscripts within rows denote tendencies ($0.05 > P \leq 0.10$).

Table 5. Effect of rearing feed restriction program on broiler breeder reproductive performance during early (25−45 wk), late lay (46−60 wk), and overall (wk 25−60).

Variable by lay period[1]	Feeding program[3] SAD	ED	SE	*P* value
Egg production, %				
Early lay	67.3	66.0	2	0.627
Late lay	59.9	58.5	1	0.247
Overall	64.2	63.1	1	0.481
Hen BW, g				
Early lay	3,135[b]	3,196[a]	17	0.013
Late lay	4,051	4,057	14	0.763
Overall	3,434[b]	3,477[a]	14	0.037
Hen BW CV, %				
Early lay	11.3[a]	10.4[b]	0.3	0.046
Late lay	11.9[a]	10.2[b]	0.3	<0.001
Overall	11.5[a]	10.3[b]	0.2	0.001
Egg weight, g				
Early lay	60.6[b]	61.5[a]	0.3	0.036
Late lay	68.6	68.8	0.2	0.384
Overall	63.3[b]	64.4[a]	0.3	0.015
Egg-specific gravity, g/cm^3				
Early lay	1.0837	1.0837	0.0002	0.793
Late lay	1.0815[b]	1.0822[a]	0.0002	0.006
Overall	1.0823[y]	1.0827[x]	0.0002	0.057
Cumulative performance[1]				
Age at sexual maturity, d	176.9	174.5	1.6	0.307
Eggs per hen housed	148.7	147.9	3.8	0.879
Chicks per hen housed	133.3	132.1	3.6	0.806
Feed conversion, kg per dozen eggs	3.66	3.70	0.1	0.762
Mortality, %	8.2	6.4	1.6	0.424

[1]Sexual maturity = day each pen achieved 5% weekly egg production. Eggs per hen housed = Total pen egg production/initial hen placed (corrected for sampled birds). Chicks per hen housed = [Σ (wk pen hatchability × wk egg pen production)]/initial hens placed (corrected for sampled birds). Feed conversion = total pen feed/total pen egg production.

[3]Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen; and ED = everyday feeding regimen. All birds were fed daily through lay starting at wk 21.

[a,b]Means with different superscripts within rows denote significant differences ($P \leq 0.05$).

[x,y]Means with different superscripts within rows denote tendencies ($0.05 > P \leq 0.10$).

Table 6. Effect of rearing feed restriction program on broiler breeder fertility, hatchability, and incubation performance during early lay (27−45 wk), late lay (46−60 wk), and overall (wk 27−60).

Variable by wk period[1]	Feeding program[2] SAD	ED	SE	*P* value
Fertility, %				
Early lay	97.6	97.7	0.3	0.750
Late Lay	97.6	97.0	0.4	0.322
Overall	97.6	97.4	0.3	0.609
Hatchability, %				
Early lay	92.1	92.7	0.5	0.394
Late Lay	89.3	90.2	0.8	0.418
Overall	90.9	91.6	0.5	0.256
Hatch of fertile, %				
Early lay	94.4	94.9	0.4	0.403
Late Lay	91.5	93.0	0.7	0.110
Overall	93.1[y]	94.1[x]	0.4	0.088
Early dead, %				
Early lay	2.6	2.7	0.3	0.893
Late lay	3.8	3.5	0.4	0.567
Overall	3.1	3.0	0.3	0.718
Mid dead, %				
Early lay	0.2	0.2	0.1	1.000
Late lay	0.2	0.1	0.1	0.540
Overall	0.2	0.1	0.1	0.689
Late dead, %				
Early lay	1.6	1.3	0.2	0.320
Late lay	2.4[x]	1.7[y]	0.3	0.082
Overall	2.0[x]	1.5[y]	0.2	0.055
Contaminated, %				
Early lay	-	-	-	-
Late lay	0.4[a]	0.0[b]	0.1	0.016
Overall	0.2[a]	0.1[b]	0.1	0.020
Dead pip, %				
Early lay	0.1[x]	0.0[y]	0.0	0.092
Late lay	0.2	0.2	0.1	0.142
Overall	0.3[a]	0.1[b]	0.1	0.036

[1]All incubation data were determined by incubating $n = 720$ eggs from each treatment at each timepoint. Cull chick, live pips, and cracked eggs % were not impacted by rearing feeding regimen ($P \geq 0.131$; data not shown).

[2]Feeding regimens were used from wk 4 to 20; SAD = skip-a-day feeding regimen; and ED = everyday feeding regimen. All birds were fed daily through lay starting at wk 21.

[a,b]Means with different superscripts within rows denote significant differences ($P \leq 0.05$).

[x,y]Means with different superscripts within rows denote tendencies ($0.05 > P \leq 0.10$).

that ED feeding improved uniformity, although in our study, birds from both groups did not differ in uniformity, similar to the results reported by de Beer and Coon (2007). Zuidhof et al. (2015) reported that ED pullets were less uniform at wk 22 compared to SAD pullets (15.3 vs. 12.7% CV). Although, Zuidhof et al. (2015) ED pullets were fed less feed from wk 15 to 21 to achieve a similar target BW compared to SAD birds, possibly affecting feed distribution, reducing feeding time and hence uniformity. Trough chain-feeders are commonly used in the United States and their slow delivery speed in long pullet houses is concerning when attempting to use a daily feeding program (Wilson, 2003). In our trial, ED feeding did not compromise bird uniformity as often believed, possibly due to the increased fiber sources in ED diets. Treatment pen uniformity became numerically closer at wk 20, which might be explained by the increases in feed allocation between wk 15 to 20, prolonging feeding time even for those fed daily. Even if mortality was not different between groups, the feed conversion per live pullet averages indicated that ED regimen was more efficient through rearing. Combining ED feeding with a special formulation did not impair BW or uniformity, although more extreme formulation changes might be necessary in larger commercial operations.

Lean muscle in these pullets accounted for 90% of their BW in rearing. Fasting can deplete liver glycogen storage making animals rely on adipose tissue and muscle to obtain energy (de Beer et al., 2007; Sanvictores et al., 2018). SAD regimen or intense restriction reduced pullet skeletal muscle accretion and breast weight compared to ED feeding (Zuidhof et al., 2015; Vignale et al., 2017). In our study, ED pullets contained more lean muscle weight compared to SAD pullets from wk 11 to 25, showing why BW differs between groups while in rearing. Sufficient carcass fat becomes critical as pullets approach photostimulation age to modulate their plasma hormone profiles such as estradiol which in part induces sexual maturation and ovulation (Renema et al., 1999b; Sun et al., 2006). In this study, an additional 31 g (35% more) of fat were measured in the body

of ED pullets compared to SAD birds at 19 wk, which is desirable as they approach lay age. Even if this difference is primarily due to BW differences, previous researchers have not detected body fat differences at similar ages, although the genetics and strains used differ from ours (Bennet and Leeson, 1989; de Beer and Coon, 2007; Vignale et al., 2017). In our study, this difference in body fat is likely due to the metabolic alterations that SAD induces. SAD induces higher circulating corticosterone after 20 h postfeeding compared to ED pullets (de Beer et al., 2008), which reduces insulin-sensitiveness and increases liver fat storage (Southorn et al., 1990; Yki-Järvinen, 2005), as observed in livers collected from SAD pullets compared to those from ED pullets (de Beer et al., 2007). Lower body fat is the result of impaired insulin sensitivity in genetically lean mice (Reitman, 2002) as well as in mice subjected to alternate-day fasting (Varady et al., 2009, 2010). These findings imply why meat-type pullets fed intermittently would have low body fat contents as compared to ED-fed pullets as shown in our study at wk 19.

Hudson et al. (1999) were the first to report that SAD regimen impairs femur growth in pullets. Similarly, initiating male breeders on SAD regimen at wk 2 or 4 decrease shank length as compared to those initiated at wk 6 (Ingram and Hatten, 2001), demonstrating that intermittent feeding impairs bone growth. Chronic hypocalcemia affects bone formation and impairs its mineralization (Mocetti et al., 2000). Field evaluations of pullet circulating ionized-Ca indicate that SAD pullets probably undergo hypocalcemia prior to the next feeding time (Clark et al., 2019), suggesting that the skeletal resorption and remodeling patterns induced by interrupted feeding would impair bone structure in SAD pullets as demonstrated in this study and as reported by Hudson et al. (1999). In growing chickens, mineral density is an indicator of the bone health status since it includes the mineral mass of the bone (Rath et al., 2000). Weak and less mineralized bones are produced from feeding Ca- and P-deficient diets to meat-type chickens (Patterson et al., 1986; Imari et al., 2020; Li et al., 2020), although pullets from our study were fed isonutritious diets (Table 1), with the formulated Ca and available P provided the same over a 2-day period. Another possible explanation for these differences in pullet bone density is the relationship between BW and bone porosity and mineralization. A greater BW in broiler-type chickens results in load-induced bone formation at the periosteal surface even when restricted from feed (Williams et al., 2004), and suggests that the greater ED pullet BW had a positive influence bone density while in rearing as compared SAD-fed pullets.

Gastrointestinal Tracts

Relative organ weights agree with those reported by Sweeney et al. (2022) with SAD feeding and Lindholm et al. (2018) where pullets were evaluated on a 5:2 (5 d of feed: 2 off) feeding regimen. Larger crops, gizzards and proventriculus in SAD birds are likely explained by the tissue distention that double portions of feed cause when using SAD feeding regimen. Crops from SAD pullets empty on the day off from feed and this is followed by higher blood corticosterone concentrations which is a stress indicator (de Beer et al., 2008). Compression-sensitive receptors that influence GIT motility are found in gizzards (Duke et al., 1977), implying that the larger feed volume given to SAD pullets could modulate this organ function compared to ED pullets. Relative liver weight of SAD pullets was greater than those of ED pullets during most of the rearing period agreeing with data from Sweeney et al. (2022) and de Beer et al. (2007). The larger livers in SAD pullets are due to the glycogen and lipid accumulation that intermittent fasting induces to maintain blood glucose on the day off (de Beer et al., 2007).

Nutrition has remarkable implications in GIT morphology and function. Goblet cells are found in the intestinal surface epithelium and produce mucins, creating the mucosal layer which offers pathogen defense and absorptive properties. Pullets fed under SAD had reduced ileal, jejunal, and duodenal villi goblet cells at most early samplings (≤10 wk), which could lead to reduced intestinal mucus contents as observed in grown broilers subjected to feed withdrawal (Thompson and Applegate, 2006). Goblet cells continuously regenerate from stem cells contained in the crypts before migrating to the villus (Zhang and Wu, 2020; Duangnumsawang et al., 2021). At each sampling, pullets were sampled prior to feeding time, meaning that SAD pullets had been off from feed for 48 h, whereas ED birds had been off for only 24 h only. Rat and chick studies revealed that 48 to 72 h of food removal induce ileal and duodenal sloughing and reduce crypt depth and cell migration, with some of these effects being reversed after refeeding (Holt et al., 1986; Shamoto and Yamauchi, 2000). In part, this clarifies why young (≤10 wk) ED pullets herein showed deeper ileal crypts and more villus goblet cells in both ileum and duodenum compared to SAD pullets. It is unclear if the higher crude fiber in the ED diets (Table 1) influenced the intestinal morphology since previous researchers have not recognized a definitive relationship between dietary crude fiber and intestinal morphology (Rahmatnejad and Saki, 2015; Tejeda and Kim, 2020), and most of these observations are conflicting among studies (Mateos et al., 2012). In a recent study from our group, Sweeney et al. (2022) fed the same diet to both ED and SAD pullets, observing a similar increase in jejunal villus length in ED pullets at 16 wk. This would imply that the feeding regime has a profound influence on jejunal villus length and explaining our similar observations. However, dietary fiber could have an influence on goblet cell populations. In Rahmatnejad and Saki (2015) study, ileal goblet cell counts were higher in broilers (21 d) fed 2 and 4% carboxymethyl cellulose as compared to control broilers. Therefore, the influence of the higher fiber content in ED pullet diets is also a plausible explanation for the early (wk 4 and 10) increase in intestinal goblet cell counts. It is recognized that fats and proteins are primarily absorbed in the jejunum in chickens (Imondi and Bird, 1965; Renner, 1965), making nutrient absorption highly dependent on

the absorption surface, which can increase with longer villi. This suggests that nutrient absorption area possibly increases in ED-fed pullets at 16 wk, and partially demonstrates why these pullets gain more weight even when fed the same nutrients on a 2-day basis as compared to SAD birds.

Breeder Reproduction

Detecting reproductive performance differences of hens previously fed under both regimens as pullets is critical to fully understand the commercial implications of these practices. Previous research shows that hens fed ED as pullets achieved sexual maturity at an earlier age (de Beer and Coon, 2007) and have higher egg production at this age compared to those fed SAD as pullets (Sweeney et al., 2022). Even if the sexual maturity results were not significant in our study, this advanced egg onset in ED hens would be the consequence of a greater BW and increased body fat (Bornstein et al., 1984; Renema et al., 1999a,b) as demonstrated in our study at wk 19. Overall egg production was unaffected by rearing feeding regimen with similar results to Sweeney et al. (2022). Heavier eggs from ED hens were also detected by Sweeney et al. (2022), and this is mainly caused by the positive influence that hen BW has on egg weight especially during early lay (Summers and Leeson, 1983; Nys, 1986). Maintaining a proper eggshell quality in older hens is crucial for successful egg collection and incubation. This egg property was improved in eggs laid by ED hens during late lay (46−60 wk) and overall. Avian medullary bone formation is concomitant to sexual maturation and is considered a Ca reservoir for eggshell formation during lay (Dacke et al., 1993). The DEXA scans are unable to provide medullary bone information or cortical bone mineralization. In our study, body bone mineral density did not differ between treatment birds while in lay (≥25 wk), although bone mineral density was higher in ED pullets prior to lay (19 wk). The individual hen oviposition cycle changes the bone mineral properties (Kerschnitzki et al., 2014), in part explaining the variability detected after 19 wk of age in hen bone mineral density (see error bars in Figure 2C). On a different note, Ca and phosphate absorption primarily happens in the jejunum (Hurwitz and Bar, 1965, 1970), and eggshell quality is influenced by Ca-binding proteins found in the intestine and shell gland (Berry and Brake, 1991). Whether daily pullet feeding assisted hen intestinal integrity and long-term mineral absorption remains unclear, but the higher bone density measured during rearing might provide adequate Ca demand for eggshell formation possibly explaining why ED hens showed higher late lay eggshell quality as demonstrated in this study.

Incubation

Pullet feeding regimen did not affect hatchability or fertility during the experiment. This is probably because male mating behavior has a substantial impact on floor pen fertility (Duncan et al., 1990), which ranged above industry standards through the entire experiment (fertility: 96−97%) and since the males placed in hen pens at wk 23 were uniform (3,352 ± 190 g of BW; 5.6% CV). Embryonic mortality influences hatch of fertile %, which in this study, tended to be higher when incubating eggs from ED hens compared to those from SAD group on average (94 vs. 93% in hatch of fertile; Table 6). The eggshell is the main barrier against gas, water, and contamination, and thinner shells allow eggs to dry more during incubation, increasing mid and late embryo mortalities, and reducing hatchability (McDaniel et al., 1979; Roque and Soares, 1994). This association between eggshell quality and incubation performance would explain why more late embryo mortalities, dead pips, and contaminated eggs were detected when incubating eggs from SAD hens, ultimately reducing the hatch of fertile %. This positive effect on incubation performance is meaningful especially as broiler chick demand continues to increase (USDA, 2022).

In summary, the results in the present study confirm that ED-fed pullets are heavier than those fed in a SAD regimen when supplied with similar nutrients over a 2-day period. This BW difference appears to be primarily in body lean muscle mass, and to some extent, body fat deposition as ED birds approach photostimulation age. Daily feeding stimulated an increased bone mineral density during rearing. Along with other studies, these events can be explained by the metabolic alterations that SAD birds undergo during intermittent fasting and refeeding periods. These data reiterate why daily feeding is more efficient by converting feed to BW mass in a feed-restricted bird. Larger gastrointestinal organs were observed in SAD pullets compared to ED hens, and this would be explained by the distention caused by double ration on the feed day. At most early pullet samplings, intestinal villus goblet cells populations were higher in daily-fed pullets, and the 16 wk jejunal villi length were longer compared to SAD-fed pullets. Together with previous research, SAD regimen affects the intestinal structure and possibly its function. Hens previously fed under both regimes in rearing did not show performance differences although those fed ED as pullets had improved eggshell quality during late lay and improved hatch of fertile %.

In conclusion, ED feeding program was more efficient for the pullet growth performance, while increasing the bone density and body fat prior to photostimulation age and without showing apparent negative effects on the gastrointestinal development when compared to pullets fed using SAD program. In addition, this study is the first to reveal that pullet ED regimen can have a positive influence on late lay eggshell quality and consequently incubation performance. Future research should focus on optimizing proper feed formulations for ED feeding regimes that can be used in common feeding systems and large pullet houses.

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DISCLOSURES

All authors declare no conflicts of interest.

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