The effect of alternative feeding strategies for broiler breeder pullets: 2. Welfare and performance during lay

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ABSTRACT Feeding broiler breeders to satiety has negative consequences on their health and reproduction. Alternative feeding strategies during rearing can improve welfare, although their implications during lay are not well understood. The objective was to examine the effect of rearing feeding treatments on the reproductive performance and feeding behavior of broiler breeders under simulated commercial conditions. At 3 wk of age, 1,680 Ross 308 pullets were allocated to 24 pens under 1 of 4 isocaloric treatments: 1) daily control diet; 2) daily alternative diet (40% soybean hulls and 1 to 5% calcium propionate); 3) 4/3 control diet (4 on-feed days, 3 non-consecutive off-feed days per week); and 4) graduated control diet. Feeding frequency of the graduated treatment varied with age and finished on a daily basis. At 23 wk of age, group sizes were adjusted to 40 hens, and 5 mature Yield Plus Males roosters were introduced to each pen. Pens were under the same daily feeding management and same diet during lay. The performance of broiler breeders (growth rate, body weight uniformity, and reproductive performance) was determined until 64 wk of age. At the end of lay, feeding motivation was examined with a feed intake test and a compensatory feeding test. Data were analyzed using linear mixed regression models, with pen nested in the models and age as a repeated measure. The laying rate of hens reared on the graduated treatment decreased slower compared to control hens, resulting in a higher cumulative egg production (178.2 ± 3.8 eggs/hen) than control hens (165.2 ± 3.8 eggs/hen, $P < 0.01$) by 64 wk of age. Hens reared on non-daily feeding treatments laid lighter eggs with relatively heavier yolks and had higher feed intake at the end of lay than hens fed daily during rearing ($P = 0.02$). In conclusion, rearing feeding treatments impacted the growth rate and body weight uniformity during lay, feeding motivation at the end of lay, and the laying rate and hatchability depending on hens' age.

Key words: reproductive performance, behavioral programming, rearing feeding treatment, alternative diet, non-daily feeding

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INTRODUCTION

Broiler breeders are the parent stock of broiler chickens and have the same genetic predisposition for fast growth and high feed intake as their progeny (Ramachandran, 2014). However, broiler breeders fed ad libitum develop obesity-related problems such as lameness, high mortality, low egg production, and low fertility rates (Katanbaf et al., 1989a,b; Bruggeman et al., 1999; Hocking et al., 2002; Heck et al., 2004). Therefore, commercial broiler breeder hens are routinely feed-restricted during rearing, starting the first week of age, to achieve reproductive performance objectives (Hocking et al., 2002) and to maintain a healthy body condition (Katanbaf et al., 1989a, b; Bruggeman et al., 1999). Yet, this feed restriction is chronic and severe depending on age, leading to chronic hunger and frustration (Hocking et al., 2001; de Jong et al., 2003; Lees et al., 2017).

Researchers have examined alternative feeding practices that can limit growth rate while reducing hunger (Sandilands et al., 2005, 2006; Nielsen et al., 2011; Morrissey et al., 2014). These practices include alternative diets and alternative feeding schedules to alleviate the high feeding motivation of broiler breeders. The development of alternative diets has focused on

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diluting calorie content in exchange for a larger feed allotment on a daily basis (D'Eath et al., 2009; van Krimpen and de Jong, 2014; van Emous et al., 2015b). We found that an alternative diet containing soybean hulls and calcium propionate reduced feeding motivation in broiler breeder pullets compared to a standard diet (Arrazola et al., 2019). Rationed alternative diets, including those that have a higher fiber content than is standard, can reduce the effects of chronic feed restriction during rearing while enabling breeders to reach a mature body weight and sexual maturity (Sandilands et al., 2005; Morrissey et al., 2014; de los Mozos et al., 2017). Alternative diets also appear to enhance reproductive performance during lay (Ramachandran, 2014; van Emous et al., 2015a; de los Mozos et al., 2017). However, the long-term effect of alternative treatments during rearing on the welfare of broiler breeders during lay is unclear.

Another alternative feeding strategy for managing broiler breeders is non-daily feeding. Non-daily feeding schedules during rearing are common on-farm practices in North America to improve body weight uniformity for broiler breeder pullets (Zuidhof et al., 2015; Carneiro et al, 2019). When compared to a daily feeding schedule, non-daily feeding reduced behavioral signs of hunger and physiological indicators of chronic stress during rearing (Morrissey et al., 2014; Arrazola et al., 2019). However, non-daily feeding is less feed-efficient than daily feeding, which may have lasting impacts on egg production if it greatly reduces growth rate compared to daily feeding (de Beer and Coon, 2007, 2009; Montiel, 2016). More research is needed to better understand the effect of rearing feeding strategies on the welfare and reproductive performance of broiler breeders through lay.

The objective of this research was to examine the effect of a rationed alternative diet and non-daily feeding schedules during rearing on the reproductive performance and feeding behavior of broiler breeders under simulated commercial conditions. Based on the results of Hocking et al. (2002) and van Emous et al. (2015a), hens reared on the alternative diet (40% soybean hulls and calcium propionate) were hypothesized to have greater reproductive performance and lower feeding motivation compared to control hens. We also predicted that the reproductive performance of control hens would be greater than hens reared on the non-daily feeding, in line with results from de Beer and Coon (2007, 2009) and Vignale et al. (2016).

MATERIALS AND METHODS

A total of 960 Ross 308 broiler breeder hens and 120 Yield Plus Males (**YPM**) broiler breeder roosters were housed at the Arkell Poultry Research Station (Guelph, ON, Canada) from July 2015 to June 2016. Hens were a subset of pullets from a previous experiment that evaluated the effect of rearing feeding strategies in broiler breeder pullets (Arrazola et al., 2019). All of the procedures in this experiment were approved by the University of Guelph's Animal Care Committee (AUP # 3141) and were in accordance with the guidelines outlined by the Canadian Council for Animal Care (CCAC, 2009).

Housing and Management

Rearing Management Chicks were donated courtesy of Aviagen (via Horizon Poultry, Hanover, ON, Canada) and were vaccinated at the hatchery based on local recommendations and the health program in the research facility. At the hatchery, chicks were beak treated using an infrared beam and toe trimmed (males only) according to industry standards. Male chicks were reared at the research facility from 1 D of age to 22 wk old in one group and managed following guidelines for specialty males (Aviagen, 2014). Females chicks were reared in 24 floor pens until 20 days old. Then, 1,680 pullets were allocated to 24 floor pens at 70 pullets per pen (7.7 pullets/m^2) controlling for body weight and body weight uniformity. The pullets were managed based on breeding company recommendations (Aviagen, 2011) and environmental conditions during rearing were maintained at 21°C room temperature and 60% relative humidity. The pullets were reared on 8L:16D light program at 21 lux from 3 to 5 wk of age and at 15 lux from 6 to 21 wk of age. The light program switched to 54 lux on 12L:12D at 22 wk of age and photoperiod increased to 13L:11D at 23 wk of age. The pullets were feed-restricted according to feed allotment suggested by Aviagen (2011). From 3 to 22 wk of age, pullets were assigned to 1 of 4 feeding strategies (i.e., treatments): (1) control diet fed daily (control); (2) alternative diet fed daily; (3) control diet fed on a 4/3 schedule; or (4) control diet fed on a graduated schedule. Further information of the rearing phase can be found in Arrazola et al. (2019).

Lay Housing and Management At 23 wk of age, 960 hens remained in their home pen (40 hens per pen and segregated by rearing treatment) and 120 twenty-three-wk-old roosters were introduced (5 roosters per pen). Only mature hens and roosters were used for this experiment and they were selected based on body weight (±15% of target body weight). Hens weighed 2652.6 ± 196.8 g and roosters weighed 3302.1 ± 414.3 g (mean ± SD) at 23 wk of age. The flock was spiked when hens were 45 wk of age, and one rooster per pen was replaced by a 25-wk-old YPM rooster reared off-site (3955.0 ± 291.7 g). Broiler breeders were managed based on breeding company guidelines (Aviagen, 2013a) to meet parent stock performance objectives for hens (Aviagen, 2011) and roosters (Aviagen, 2014), and the management practices were consistent across rearing treatments. Floor pens were 9.25 m^2 (40% scratching area with wood shavings, and 60% plastic slat area at 0.45 m above the scratching area). Broiler breeders were housed at a density of 4.9 birds/m^2 (40 hens and 5 roosters per pen), and pens were equipped with ten nest boxes (48 cm deep × 30 cm wide × 50 cm high) per pen. Water was provided ad libitum from 2 drinker lines per pen (14 nipples/pen). Two trough

Table 1. Composition of the 3 commercial broiler breeder diets provided during lay from 23 to 65 wk of age, using a 2-stage diet for hens and a grower diet for roosters.

	Hens		Roosters
Analyzed composition[1]	Layer 1[2]	Layer 2[3]	Grower
AME[4] (Mcal/kg)	2.61	2.54	2.48
Ethanol soluble (%)	3.04	4.14	3.62
Crude protein (%, N x 6.25)	16.37	16.03	14.84
Ca:P ratio	4.64	4.58	1.76
Calcium (%)	3.36	3.78	1.55
Phosphorus (%)	0.72	0.82	0.88
Sodium (%)	0.20	0.17	0.17
Potassium (%)	0.63	0.58	0.77
Magnesium (%)	0.20	0.19	0.22
Crude fat (%)	4.52	4.38	2.43
Starch (%)	38.75	36.52	40.65

[1]Analyzed at Agri-Food Laboratories (Guelph, ON, Canada).
[2]Fed from 23 to 45 weeks of age.
[3]Fed from 46 to 65 weeks of age.
[4]Apparent metabolizable energy.

feeders per pen (5 cm deep × 13 cm wide × 152 cm long with rooster-exclusion grills; feeder space at 15 cm/hen) were used for hens on the slatted area, and 1 round feeder per pen (feeder space at 15 cm/rooster) was used for roosters 60 cm above the ground on the scratching area. Broiler breeders were fed daily at the restricted feed allotment recommended for hens (Aviagen, 2011) and roosters (Aviagen, 2014) to meet nutritional specifications. Beginning at 23 wk of age, hens were on a 2-phase broiler breeder layer feeding program (a broiler breeder layer 1 from 23 to 45 wk old, and a broiler breeder layer 2 from 46 to 64 wk old; Table 1) without a pre-breeder diet, and roosters were fed a grower diet (Table 1). Particle size was medium crumble for all diets. Room temperature remained at 21°C and relative humidity decreased from 74% at 23 wk of age to 43% at 64 wk of age. Lights came on at 08:00 at 54 lux for 13L:11D from 23 wk of age onwards, and birds were fed at 08:30. Mortality was recorded as it occurred, and weak, lame, and/or severely injured broiler breeders were euthanized by cervical dislocation.

Experimental Design

Treatments were applied during rearing using a randomized block design with 4 feeding treatments and 6 replicates per treatment. Pens were in 4 rooms and all treatments were represented in each room. The experimental design controlled for location within room (side, location, and neighbor treatment). The control diet was formulated according to nutritional specifications (Aviagen, 2013b), and the alternative diet was a dilution of the control diet with 40% soybean hulls at a fixed inclusion rate, and with calcium propionate at 1.44, 3.19, and 5.05% in the starter, grower 1, and grower 2 diets, respectively. Control pullets were fed the control diet daily; pullets on the 4/3 and the graduated schedules were fed the control diet on a non-daily feeding schedule. Pullets on the 4/3 schedule were fed 4 days per week (on-feed days), with 3 non-consecutive off-feed days per week. Pullets on the graduated schedule were fed on a varying feeding frequency based on the pullets' age. The graduated schedule had a 5/2 schedule (5 on-feed days per week; 2 non-consecutive off-feed days per week) from weeks 3 to 4, a 4/3 schedule from weeks 5 to 11, a 5/2 schedule from weeks 12 to 18, and daily from weeks 19 to 22. All treatments provided the same apparent metabolizable energy per week. See Arrazola et al. (2019) for further information.

Data Collection

Body Weight and Body Weight Uniformity All hens and roosters were weighed after daily feed consumption at weeks 23 and 65. A fixed subsample of 10 focal hens per pen (wing-tagged and dye-identified [concentrated gel colors, Wilton Industries, Woodridge, IL]) and all roosters were individually weighed biweekly (i.e., every other week) starting at 25 wk of age. Body weight uniformity is presented as the coefficient of variation (**CV**), calculated by dividing the standard deviation of body weight by the average body weight per pen.

Egg Production Eggs were collected daily from 23 to 64 wk of age at 09:00 after hens were fed. The location of each egg was noted as floor or nest, and the eggs found in the scratching area or on the slats were defined as *floor eggs*. Egg production was categorized into early lay (23 to 27 wk of age), peak (28 to 33 wk of age), mid lay (34 to 49 wk of age), and late lay (50 to 64 wk of age). The incidence of abnormal eggs such as double-yolk eggs and soft-shell eggs was not estimated, although abnormal eggs were rarely observed throughout lay. For incubation purposes, researchers collected eggs once per week and every 4 wk beginning at 28 wk of age. The eggs were sorted based on settable egg criterion. The eggs that were heavier than 52 g and were not double-yolked, cracked, dirty or warm at the time of collection were defined as *settable eggs*. Floor eggs and dirty eggs (i.e., eggs with fecal material covering an area greater than 0.25 cm^2) were discarded. Settable eggs were individually weighed to estimate egg weight and egg weight uniformity. The CV of egg weight was calculated by dividing the standard deviation of egg weight by the average egg weight per pen. A subsample of 5 settable eggs per pen were cracked for egg component analysis (shell, albumen, and yolk weight) when hens were 56, 60, and 64 wk of age. Albumen weight was calculated by subtracting yolk and shell weight from the settable egg weight.

Fertility, Hatch of Fertile, and Hatchability A total of 12 settable eggs were selected per pen and hens' age for incubation. Settable eggs received a unique blind code after recording initial egg weight and were stored in a cooler at 15.5°C during 4 D before incubation. Eggs laid at 28, 36, 44, 52, and 60 wk of age were incubated for 7 D, whereas those laid at 32, 40, 48, 56, and 64 wk were incubated to hatch. Settable eggs were kept separated by parent pen and controlling for location within the setter and the hatcher among treatments. No disinfection procedure or in ovo vaccination was applied to the hatching eggs. The eggs incubated for 7 D were individually weighed, candled, and then cracked to assess fertility (based on germinal disk criterion; Watt et al., 1993) and embryo mortality after 1 wk of incubati*on. Fertility* was calculated by dividing the number of fertile eggs by the number of settable eggs, and the *relative egg weight loss* was calculated by subtracting initial egg weight from final egg weight and then dividing by the initial egg weight. The eggs incubated to hatch remained in the setter until day 18 of incubation, and only fertile eggs were transferred to the hatcher after candling. Settable eggs were incubated at 37.5°C and 55% relative humidity at 24 turns per day in the setter and at 37.5°C and 75% relative humidity in the hatcher. Hatchability was determined at 21.5 D of incubation, and the remaining (unhatched) eggs were cracked to assess fertility and embryo mortality. Hatchability was calculated by dividing the number of live chicks that hatched by the number of settable eggs, and hatch of fertile (**HOF**) was calculated by dividing the number of hatching eggs by the number of settable eggs. Eggs from which a chick hatched were defined as *hatching eggs*. Contaminated eggs and yolk infections were identified as they occurred. Chicks were individually weighed, and feather-sexed at the hatchery.

Feeding Motivation: Feed Intake Test and Compensatory Feeding Test Feeding motivation was estimated at 65 wk of age using a feed intake test and a compensatory feeding test. A feed intake test was performed in the home pen 1 wk after rooster removal and before hen depopulation. Hens were fed at their daily feed allotment and the remaining feed was weighed 1 h after being fed (i.e., 1 h after feed was provided). Individual feed intake was estimated by dividing the total feed intake in 1 h by the number of hens per pen. Hens were weighed after the feed intake test, and the relative feed intake in 1 h was calculated by dividing feed intake by average body weight.

At 65 wk of age, 5 hens per pen were randomly selected from the 10 focal hens per pen for a compensatory feeding test. These hens remained in their home pen after depopulation of the other hens and were fed ad libitum for 48 h. A round feeder was filled with 4 kg of the home diet (broiler breeder layer 2 diet). Hens and feeders were weighed before and after the compensatory feeding test. The compensatory body weight gain was calculated by subtracting the initial body weight from the body weight 48 h after ad libitum feeding.

Statistical Analyses

The effect of rearing treatments on the reproductive performance and behavior of the broiler breeders was analyzed using generalized linear mixed models, with pen nested in the models as the independent experimental unit. Statistical analyses were performed using SAS Ver. 9.4 (SAS Institute, Cary, NC) with the GLIMMIX procedure and the significance level was set at *P*-values less than 0.05.

Rearing treatment, age, and their interaction were included as fixed effects for each model. Room, pen, and pen location within the room were included in the covariance structure as random effects. Age was fit into a repeated structure with pen as the subject, and treatment as the group. Contrast statements were used to examine the overall effect of diet (the alternative diet vs the control diet [the control treatment, the 4/3 treatment, and the graduated treatment]), feeding frequency (daily [the control treatment] vs non-daily [the 4/3 treatment and the graduated treatment]), and the alternative treatments ([the alternative diet, the 4/3 schedule, and the graduated schedule] vs the control treatment). Pairwise comparisons between treatments were adjusted for multiple comparisons using the Tukey test. Orthogonal regressions analyzed the effect of age into a linear, quadratic, cubic, and lack of fit response. Model assumptions were assessed using a scatterplot of studentized residuals, linear predictor for linearity, and a Shapiro-Wilk test for normality. The effect of the body weight of the roosters on fertility, hatchability, and the HOF was also analyzed using partial Pearson correlations, with age as a partial factor, and a covariate in the model. The effect of the body weight of hens on the percentage of male chicks at hatch was analyzed as a covariate in the model at the end of laying. The effect of treatments on the average chick weight and chick weight CV was also analyzed including hatching egg weight and the CV of hatching egg weight, respectively, as a covariate in the model.

RESULTS

Hens were fed in accordance with breeding company guidelines; however, feed allotment was consistently (i.e., across all treatment groups) lowered by 1.4 g per hen per day from 45 to 54 wk of age due to hens exceeding their target body weight (Aviagen, 2011). Mortality and culls were less than 8% for hens and 9% for roosters during lay. Data are presented using estimated mean values followed by the standard error of the mean.

Body Weight and Body Weight Uniformity

Hens The body weight of the hens was affected by the rearing treatment ($F_{3,393}$ = 11.36, $P < 0.001$) and increased over time following a cubic curvature ($F_{1,393}$ = 13.58, $P < 0.001$). Hens reared on the alternative diet were lighter than hens reared on the control treatment throughout lay (Figure 1; t_{393} = 4.15, $P < 0.001$). The CV for hens' body weight during lay was affected by the rearing treatment ($F_{3,393}$ = 6.89, $P < 0.001$) and age ($F_{19,393}$ = 9.47, $P < 0.001$). Hens reared on the 4/3 schedule had lower body weight CV (7.3 ± 0.4%) than hens reared on the control treatment (8.3 ± 0.4%; t_{393} = 3.76, $P = 0.001$), the alternative diet (8.4 ± 0.4%; t_{393} = 3.41, $P = 0.004$), and the graduated schedule (8.5 ± 0.4%; t_{393} = 4.30, $P < 0.001$).

Roosters The body weight of roosters was associated with the hens' rearing treatment ($F_{3,393}$ = 35.68, P <0.001), although no treatment was applied to roosters and roosters were all reared under identical

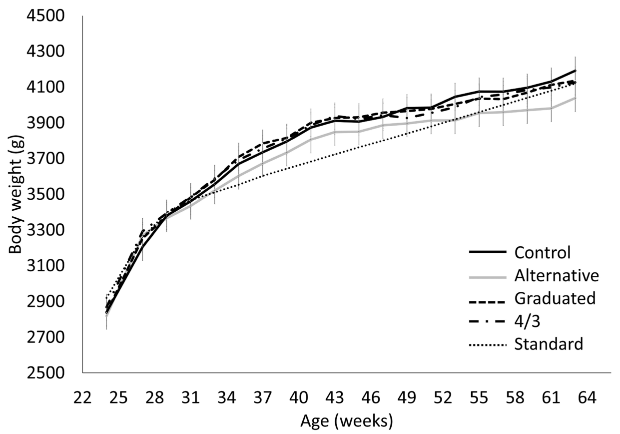

Figure 1. The effect of diet and feeding frequency during rearing (control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule) on hens' growth rate during lay (mean ± SE). Rearing treatments ended at 22 wk of age, and the hens' feeding management was the same across treatments during lay. The dotted line refers to Ross 308 broiler breeder performance objectives (Aviagen, 2011). Hens fed the alternative diet during rearing (gray solid line) were lighter than those fed the control diet daily (black solid line; $P < 0.001$).

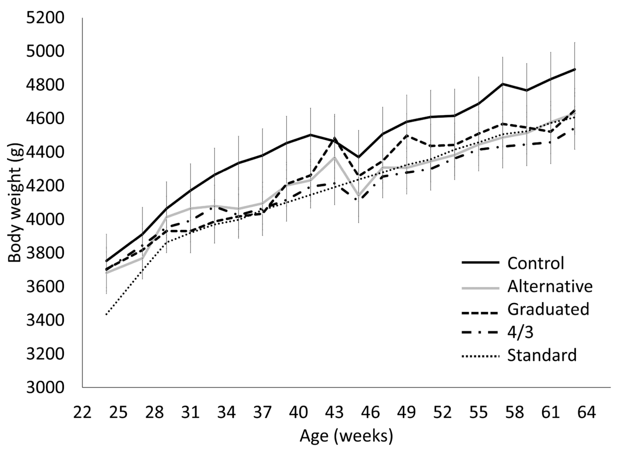

Figure 2. The growth rate of roosters (mean ± SE) housed with hens reared under 4 different feeding strategies (control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule). Rearing treatments ended at 22 wk of age, and no treatment was applied to the roosters. At 45 wk of age, 1 rooster per pen was replaced by a 25-wk-old rooster. The dotted line refers to the YPM specialty male performance objectives (Aviagen, 2014). Roosters housed with hens reared on the control diet (black solid line) were heavier than those housed with hens reared on the 4/3 schedule (dashed dotted line; $P < 0.001$) and the graduated schedule (dashed line; $P < 0.02$).

conditions (Figure 2). Roosters housed with hens reared on the 4/3 schedule were 68.6 ± 21.3 g lighter compared to those housed with hens reared on the graduated schedule ($t_{393} = 2.95$, $P = 0.02$). Roosters housed with hens reared on the control treatment were consistently heavier (225.3 ± 29.7 g) than roosters housed with hens reared on the 3 alternative treatments (combination of the alternative diet, the 4/3 schedule, and the graduated schedule; $F_{1,393} = 60.47$, $P < 0.001$). The CV for roosters' body weight was affected by the rearing treatment of the hens ($F_{3,393} = 9.88$, $P < 0.001$) and the roosters' age ($F_{19,393} = 3.07$, $P < 0.001$). The body

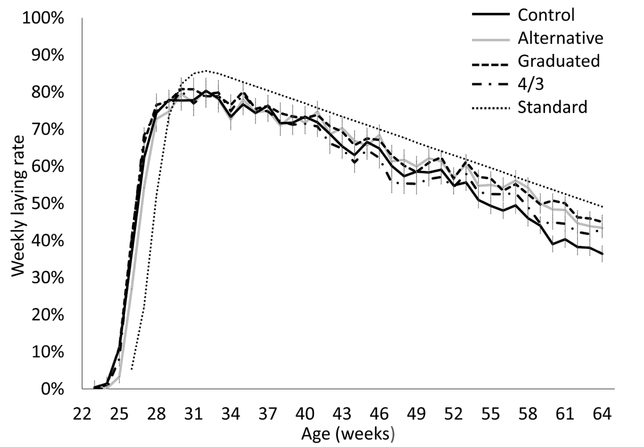

Figure 3. The effect of diet and feeding frequency during rearing (control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule) on percentage of daily egg production per hen (mean ± SE). Rearing treatments ended at 22 wk of age, and the hens' feeding management was the same across treatments during lay. The dotted line refers to Ross 308 broiler breeder performance objectives (Aviagen, 2011). The effect of rearing treatment on egg production depended on the hens' age ($P < 0.01$).

weight CV was higher in roosters housed with hens reared on the alternative diet (13.4 ± 0.9%) than roosters housed with hens reared on other rearing treatments (combination of the control treatment, the 4/3 schedule, and the graduated schedule: 10.6 ± 0.5%; $F_{1,393} = 28.93$, $P < 0.001$).

Reproductive Performance

Egg Production Figure 3 illustrates the effect of rearing treatment and age on the laying rate by phase. The onset of egg production differed across rearing treatments ($F_{12,80} = 4.87$, $P < 0.001$). At 26 wk of age, the laying rate was 9.7 ± 2.4% lower in hens reared on the alternative diet compared to those reared on the control treatment (Figure 3; $t_{80} = 3.97$, $P = 0.02$). Nevertheless, hens in all treatments reached similar peak egg production at 31 wk of age ($F_{3,114} = 0.70$, $P = 0.55$). Then, weekly egg production per hen was affected by the rearing treatment and age during mid lay ($F_{45,297} = 1.47$, $P = 0.03$). From 43 to 48 wk of age, hens reared on the 4/3 schedule had lower laying rate (60.57 ± 1.71%) than hens reared on the alternative diet (65.7 ± 1.7%; $t_{297} = 2.35$, $P = 0.02$). During late lay, the laying rate was influenced by age and rearing treatment ($F_{42,280} = 1.57$, $P = 0.02$). Hens reared on the control treatment had lower laying rate (10.6 ± 2.3% lower) after 60 wk of age compared to hens reared on the graduated schedule ($t_{280} = 4.71$, $P = 0.01$). The egg production of hens reared on the control treatment (46.9 ± 1.6%) decreased faster than hens reared on the alternative diet (53.9 ± 1.6%; $t_{280} = 3.32$, $P < 0.001$) and the graduated schedule (54.1 ± 1.6%; $t_{280} = 4.07$, $P < 0.001$) during late lay. The rearing treatments impacted the cumulative egg production at the end of lay ($F_{14,294} = 30.90$, $P < 0.001$). Hens reared on the graduated schedule laid more eggs per hen (178.2 ± 3.8 eggs/hen) than hens

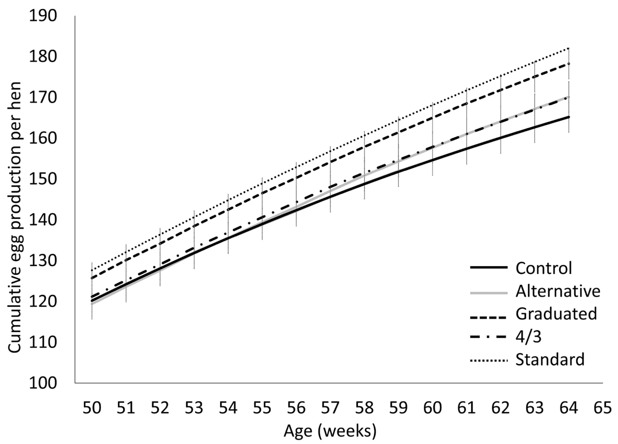

Figure 4. The effect of diet and feeding frequency during rearing (control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule) on the cumulative weekly egg production per hen during late lay (mean ± SE). Rearing treatments ended at 22 wk of age, and the hens' feeding management was the same across treatments during lay. The dotted line refers to Ross 308 broiler breeder performance objectives (Aviagen, 2011). During late lay, cumulative egg production was higher for hens reared on the graduated schedule (dashed line) compared to those on the daily control diet (black solid line, $P < 0.01$).

reared on the control treatment (165.2 ± 3.8 eggs/hen; $t_{294} = 4.59$, $P < 0.01$) by 64 wk of age (Figure 4).

Floor Eggs The percentage of floor eggs varied based on the rearing treatment and hens' age: until 25 wk of age ($F_{6,40} = 8.43$, $P < 0.001$) and afterwards ($F_{114,758} = 1.51$, $P = 0.001$). The percentage of floor eggs was lower at the onset of lay in hens reared on the alternative diet (8.8 ± 0.9%) compared to hens reared on the other 3 treatments (11.8 ± 0.9%; $F_{1,40} = 2.14$, $P = 0.043$). After 25 wk of age, the percentage of floor eggs was higher for hens reared on the alternative diet (4.0 ± 0.7%) compared to those reared on the graduated schedule (2.4 ± 0.6%; $t_{758} = 1.89$, $P = 0.031$).

Settable Eggs, Hatching Eggs, and Live Chicks The weight of hatching eggs was affected by rearing treatment (Table 2; $F_{3,21} = 2.84$; $P = 0.046$) and increased over time ($F_{4,80} = 354.57$; $P < 0.001$). Hatching eggs laid by control hens (69.25 ± 0.34 g) were heavier compared to eggs laid by hens fed non-daily during rearing (combination of the 4/3 schedule and the graduated schedule: 68.14 ± 0.34 g; $F_{1,21} = 7.27$, $P <$ 0.001). However, average chick weight was not impacted by rearing treatment ($F_{3,79} = 0.73$, $P = 0.54$) nor by rearing feeding frequency (daily control diet vs non-daily control diets; $F_{1,79} = 0.11$, $P = 0.74$). The CV of hatching egg weight was affected by rearing treatment (Table 2; $F_{3,80} = 3.52$, $P = 0.02$) and age ($F_{4,80} = 6.52$, $P = 0.001$). Hens reared on the 4/3 schedule laid hatching eggs with lower egg weight CV than those laid by control hens (Table 2; $t_{1,80} = 2.90$; $P = 0.025$). The CV of chick weight at hatch was affected by rearing treatment ($F_{3,21} = 3.17$, $P = 0.038$) and age ($F_{4,60} = 6.52$, $P < 0.001$). Chicks hatched from eggs laid by hens fed non-daily during rearing (combination of the 4/3 schedule and the graduated schedule) had lower chick weight CV (6.98 ± 0.25%) compared to those from eggs laid by control hens (7.94 ± 0.33%; $F_{1,60} = 9.37$, $P = 0.007$). The effect of the rearing treatment on the CV of chick weight was associated with the CV of the hatching egg weight among rearing treatments ($F_{1,59} = 85.25$, $P <$ 0.001).

Table 2. The overall effect of diet and feeding frequency during rearing[1] on egg and chick weights (mean ± SE).

	Control	Alternative	Graduated	4/3
Weight (g)				
Settable egg[2]	68.1 ± 0.4	68.0 ± 0.4	67.6 ± 0.4	67.3 ± 0.4
Hatching egg[3]	69.2 ± 0.3[a]	68.4 ± 0.3[a,b]	68.1 ± 0.3[b]	68.1 ± 0.3[b]
Chick[4,5]	45.2 ± 0.3	45.1 ± 0.3	44.8 ± 0.3	45.3 ± 0.2
CV (%)[5]				
Settable egg[2]	6.5 ± 0.2[a]	6.3 ± 0.2[a,b]	6.2 ± 0.2[a,b]	5.8 ± 0.2[b]
Hatching egg[3]	6.5 ± 0.4[a]	5.7 ± 0.3[a,b]	5.3 ± 0.3[a,b]	5.2 ± 0.3[b]
Chick[4,5]	7.9 ± 0.3[a]	7.5 ± 0.3[a,b]	6.9 ± 0.3[b]	7.1 ± 0.3[a,b]

Control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule.

[a,b]Different superscripts within a row indicate significant pairwise differences between treatment means ($P < 0.05$).

[1]Rearing treatments ended at 22 wk of age, and the feeding management was the same across treatments during lay.

[2]Collected from hens at 28, 32, 36, 40, 44, 48, 52, 56, 60, and 64 wk of age.

[3]Collected from hens at 32, 40, 48, 56, and 64 wk of age.

[4]Hatched at 32, 40, 48, 56, and 64 wk of age of hens.

[5]Uniformity is presented as the coefficient of variation (%).

Hatching Egg Weight Loss and Egg Components Egg weight loss was not affected by rearing treatment ($F_{3,21} = 1.40$, $P = 0.25$), although it was affected by the hens' age ($F_{4,80} = 587.52$, $P < 0.001$). The relative egg weight loss increased from 2.70 ± 0.08% at 28 wk of age to 6.18 ± 0.08% at 36 wk of age ($t_{79} = 24.52$, $P < 0.001$) and then remained unchanged until the end of lay. The relative yolk weight was affected by rearing treatment ($F_{3,21} = 2.77$, $P = 0.048$), and hens fed non-daily during rearing laid eggs with a relative heavier yolk (31.9 ± 0.3%) compared to hens fed daily during rearing (combination of the control and the alternative treatment: 30.9 ± 0.3%; $F_{1,21} = 5.50$, $P = 0.03$). The relative eggshell weight remained unaffected by rearing treatment ($F_{3,21} = 1.10$, $P = 0.39$) or age ($F_{2,71} = 1.90$, $P = 0.16$). The egg weight of the subsample of eggs used for egg component analysis did not differ by rearing treatment ($F_{3,21} = 0.76$, $P = 0.55$) or by rearing feeding frequency ($F_{1,23} = 1.12$, $P = 0.29$).

Fertility, HOF, and Hatchability The rearing treatment and the age at which settable eggs were laid affected fertility ($F_{27,179} = 1.85$, $P = 0.01$), the percentage of HOF (Figure 5B; $F_{12,120} = 2.62$, $P = 0.02$), and hatchability (Figure 5C; $F_{12,120} = 2.00$, $P = 0.03$). Fertility decreased linearly for all treatments ($F_{1,179} = 4.49$, $P = 0.035$), but fertility decreased faster in hens reared on the 4/3 schedule compared to those on the graduated schedule during and after mid laying (Figure 5A; $P < 0.05$). For hens reared on the control treatment, the percentage of HOF was lower in eggs laid at 48 wk of age (75.3 ± 2.1%) compared to 32 (93.4 ± 4.1%; t_{120}

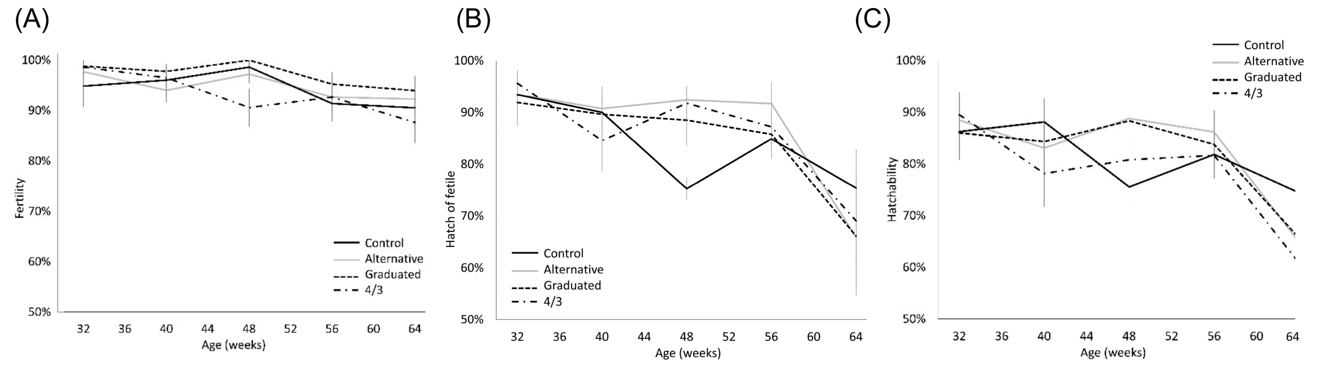

Figure 5. The effect of diet and feeding frequency during rearing (control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule) on fertility (A), hatch of fertile (B), and hatchability (C). Hatchability was calculated as the percentage of hatchlings by the number of settable eggs (%; mean ± SE). Rearing treatments ended at 22 wk of age, and the hens' feeding management was the same across treatments during lay. Rearing treatment and hens' age affected fertility, hatch of fertile, and hatchability ($P = 0.01$, $P < 0.01$, and $P = 0.03$, respectively).

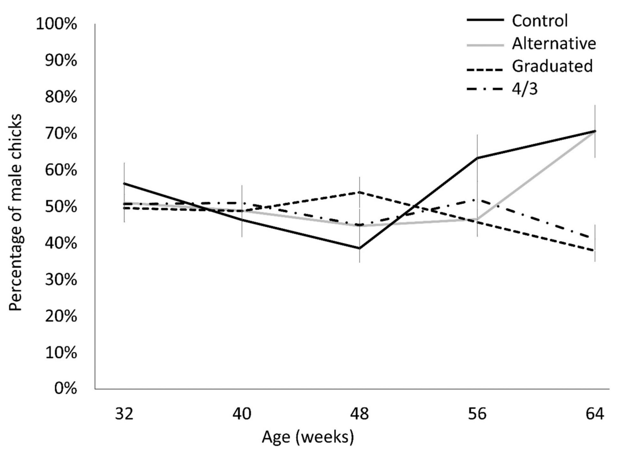

Figure 6. The effect diet and feeding frequency during rearing (control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule) on the sex ratio of the progeny of broiler breeder hens. The sex ratio of the progeny is expressed as the percentage of male chicks at hatch (mean ± SE). Rearing treatments ended at 22 wk of age, and the hens' feeding management was the same across treatments during lay. The effect of feeding frequency (daily [solid lines] vs non-daily feeding [dashed lines]) on the percentage of male chicks at hatch depended on the hens' age ($P = 0.03$).

= 4.35, $P = 0.004$) and 40 wk of age (90.0 ± 2.6%; $t_{120} = 5.57$, $P < 0.0001$). At 48 wk of age, the percentage of HOF was higher for the eggs from hens reared on the alternative diet (92.4 ± 2.4%; $t_{120} = 7.04$, $P < 0.0001$) and the 4/3 schedule (91.8 ± 3.2%; $t_{120} = 4.96$, $P < 0.001$) compared to those from hens reared on the control treatment. At 48 wk of age, hatchability was lower in eggs from hens reared on the control treatment (75.6 ± 3.5%) compared to those from hens reared on the alternative diet (88.8 ± 2.8%; $t_{120} = 5.96$, $P < 0.001$). The body weight of roosters was negatively correlated with fertility (r = –0.18, $P = 0.038$), HOF (r = –0.16, $P = 0.045$), and hatchability (r = –0.25, $P = 0.002$).

Progeny Sex Ratio The effect of rearing treatment on the percentage of male chicks at hatch depended on hens' age (Figure 6; $F_{12,104} = 2.06$, $P = 0.031$). At 64 wk of age, the percentage of male chicks was higher in eggs from hens fed daily during rearing (combination of the control treatment and the alternative diet: 67.4 ± 4.1%) compared to those from hens fed non-daily during rearing (combination of the graduated and the 4/3 schedules: 37.9 ± 4.2%; $t_{104} = 4.38$, $P = 0.001$). In addition, the heavy body weight of hens at the end of the laying was associated with a lower proportion of male chicks hatched from eggs laid at 64 wk of age ($F_{1,24} = 17.96$, $P < 0.001$).

Feeding Motivation: Feed Intake Test and Compensatory Feeding Test

Table 3 shows the effect of rearing treatment on the feeding motivation of hens at 65 wk of age according to the feed intake test and the compensatory feeding test. Rearing treatment affected the feed intake in 1 h at 65 wk of age ($F_{3,21} = 13.87$, $P < 0.001$); the relative feed intake of hens reared on the control treatment (1.35 ± 0.26%) was lower compared to hens reared on the 3 alternative treatments (combination of the alternative diet, the 4/3 schedule, and the graduated schedule: 1.93 ± 0.16%; $F_{1,21} = 31.02$, $P < 0.001$). Rearing treatments also affected the compensatory body weight gain after 48 h of ad libitum feeding ($F_{3,21} = 3.24$, $P = 0.041$), and the compensatory body weight gain of hens reared on the 4/3 schedule was higher compared to hens reared on the graduated schedule (Table 3; $t_{21} = 3.11$, $P = 0.023$).

DISCUSSION

The purpose of this research was to examine the effect of alternative feeding strategies for broiler breeder pullets during rearing on the reproductive performance and feeding behavior of broiler breeders during lay under simulated commercial conditions. Hens reared on the alternative diet were hypothesized to have greater reproductive performance and lower feeding motivation compared to control hens (Hocking et al., 2002; Enting

Table 3. The long-term effect of diet and feeding frequency during rearing[1] on the feeding motivation of 65-wk-old broiler breeder hens (mean ± SE).

	Control	Alternative	Graduated	4/3
Relative feed intake (%)[2]	1.35 ± 0.21[b]	1.88 ± 0.31[a,b]	1.78 ± 0.28[a,b]	2.12 ± 0.28[a]
Compensatory body weight gain (%)[3]	4.19 ± 1.16[a,b]	4.53 ± 1.18[a,b]	3.09 ± 0.47[b]	4.93 ± 0.59[a]

Control: control diet fed daily; alternative: alternative diet fed daily; graduated: control diet fed on a graduated schedule; 4/3: control diet fed on a 4/3 schedule.

[a,b]Different superscripts within a row indicate significant pairwise differences between treatment means ($P < 0.05$).

[1]Rearing treatments ended at 22 wk of age, and the feeding management was the same across treatments during lay.

[2]Feed intake in 1 h relative to initial body weight.

[3]Body weight gain after 48 h of ad libitum feeding divided by initial body weight.

et al. 2007; van Emous et al. 2015a), whereas those reared under non-daily feeding were predicted to have lower laying rate (de Beer and Coon, 2007, 2009; Vignale et al., 2016). Our results indicate that the reproductive performance of hens reared on the alternative diet was similar to control hens, and the effect of rearing feeding frequency on the reproductive performance of broiler breeders differed between non-daily feeding treatments throughout lay.

Body Weight and Body Weight Uniformity

The lighter body weight in hens reared on the alternative diet can indicate differences between live body weight and carcass weight at the end of rearing. During rearing, growth rate was similar between pullets fed the alternative and control diet daily (Arrazola et al., 2019). Pullets were weighed after being fed, and their heavier gastrointestinal content (due to larger feed allotment) may have masked actual differences in empty body weight and carcass weight during rearing. Laying rate can be a major determining factor of hens' body weight during lay (Renema et al., 2007); however, the laying rate of hens reared on the control treatment decreased faster than others without an effect on body weight. A higher laying persistency has been reported in hens under qualitative feed restriction during rearing compared to either ad libitum feeding (Hocking et al., 2002) or restricted feeding (van Emous et al., 2015a). This higher laying persistency was evident after 35 (Hocking et al., 2002) and 49 wk of age (van Emous et al., 2015a) compared to their restrictive control group without differences in hen's body weight, in agreement with our results. The effect of the rearing feeding strategy of the pullets on the body weight uniformity of the hens may be associated with the feeding motivation of the hens. Previous studies did not find a significant effect of qualitative feed restriction during rearing on the proportion of time feeding (Hocking et al., 2002; Sandilands et al., 2005) or clean-up time (van Emous et al., 2015b). Pullets might have learnt to be quicker eaters, but only the pullets on the fixed 4/3 feeding schedule during rearing showed a long-term higher feeding motivation than control hens. The effect of rearing feeding frequency on hens' body weight uniformity may explain the better egg weight uniformity and chick body weight uniformity laid by hens reared on the 4/3 compared to eggs laid by hens reared on the control treatment.

Laying Rate

The growth rate of pullets during rearing and body composition at the onset of lay are the main determining factors of laying rate (onset, peak, and persistency) in broiler breeders (de Beer and Coon, 2007, 2009; Walzem and Chen, 2014). Certainly, broiler breeder hens require an optimal proportion of protein and fat content at a mature body weight to uniformly stimulate and maintain laying rate (Renema et al., 2001a; Vignale et al., 2016). Rearing feeding strategies are critical to ensure that the flock simultaneously achieves sexual maturity at a mature body weight (Zuidhof et al., 2015; de los Mozos et al., 2017), although little attention has been paid to the long-lasting effects of rearing feeding strategies. Previous research has found that non-daily feeding during rearing may delay the onset of lay and peak production, and lower cumulative egg production (de Beer and Coon, 2007), although this may be due to lower body weights and feed efficiency of non-daily feeding schedules (Zuidhof et al., 2015). We did not find a similar effect on egg production, as only mature hens within 15% of target body weight were selected for this study. Hens reared on the graduated treatment showed the greatest laying persistency and the highest cumulative settable egg production. The hens reared on the graduated treatment had compensatory growth when the feeding frequency switched from non-daily to daily feeding during late rearing (Arrazola et al., 2019), and we hypothesize that the compensatory growth of pullets after switching from non-daily to daily feeding before photostimulation can enhance the laying rate persistency due to a leaner body composition.

Hens were above target body weight during mid lay before feed allotment was readjusted to meet target body weight. A heavy body weight during mid lay has been shown to decrease laying rate (Chen et al., 2006; Renema et al., 2007), but laying rate only declined significantly for hens reared on the 4/3 schedule compared to the alternative diet during this period. Hens reared on the alternative diet might have had greater laying persistency due to the delay in laying onset compared to those reared on the 4/3 schedule. Alternatively, hens reared on the 4/3 schedule might have been more efficient due to metabolic programming during rearing. The long-lasting effect of feed restriction on hepatic lipogenesis activity has been previously described (Richards et al., 2003), and others have noted that hepatic lipogenesis was higher in hens reared on a 4/3 schedule compared to control (de Beer and Coon, 2009), resulting in a higher fat retention at the end of lay for the hens reared on a non-daily schedule (Vignale et al., 2016). Therefore, hens reared on the 4/3 schedule could be more susceptible than other hens to lipotoxicity when there are slight deviations from target body weight due to metabolic programming during rearing (Chen et al., 2006; Walzem and Chen, 2014).

The delay in the onset of lay for hens reared on the alternative diet resulted in a lower egg production during early lay compared to the other rearing treatments, in agreement with Morrissey et al. (2014). Hens in all treatments switched to a control broiler breeder layer diet without a transition diet at 22 wk of age. At this time, the pullets on the alternative treatment switched from a diluted diet to a control diet from rearing to lay, and they may have required time to habituate to the novel diet, resulting in a delay in egg production. Nevertheless, a delay in egg production was not observed when pullets fed an alternative diet ad libitum gradually switched to a control layer diet with a transition period (Sandilands et al., 2005). The pullets in our study achieved mature body weight by the end of rearing and the percentage of mature pullets did not differ between rearing treatments after photostimulation at the end of rearing (Arrazola et al., 2019). Indeed, hens reared on the alternative diet reached the peak of egg production at the same time as the other rearing treatments, and the cumulative egg production did not differ from the control treatment at the end of lay. The delay in the onset of egg production might indicate a habituation to the new diet, but hens were able to compensate for this dietary transition similar to Renema et al. (2001b) and Enting et al. (2007).

Egg and Live Chick Weight

Hens reared on non-daily treatments laid lighter (but on target) hatching eggs than control hens, but without an effect of rearing treatment on live chick body weight. The effect of rearing feeding frequency (i.e., daily vs non-daily feeding) on egg weight was previously observed but in the opposite direction than our results. de Beer and Coon (2007) noted heavier eggs laid by hens reared on a 5/2 schedule compared to hens reared on a 4/3 schedule, skip-a-day and on the control treatment. However, Carneiro et al. (2019) also noted that hens reared on a 4/3 or 5/2 schedule laid lighter eggs than control hens. All hens were fed the same layer diet and feeding frequency in both studies, and the growth rate of hens did not differ according to the rearing feeding frequency. Thus, the effect on settable egg weight was not associated with laying management, and the skeletal frame size may explain the difference in egg weight during lay (de Beer and Coon, 2007, 2009). Skeletal frame size is indirectly assessed by measuring the body ash content, and keel and shank length (Leeson and Summers, 1982; Bennett and Leeson, 1989; Zuidhof et al., 2015), and pullets that were feed-restricted non-daily had shorter keels and shanks, and lower body ash content compared to those feed-restricted every day during rearing (Leeson and Summers, 1982; de Beer and Coon, 2007, 2009). However, the side effect of non-daily feeding on the reproductive performance is unclear. Pullets reared on non-daily feeding schedules were lighter during rearing in our experiment (Arrazola et al., 2019), although hens were selected based on 15% target body weight at the beginning of the laying phase. de Beer and Coon (2007) reported that pullets reared on the 4/3 schedule (at same weekly feed allotment) had lower relative body ash content and shorter keel bones before photostimulation compared to pullets reared on the 5/2 schedule. This difference might suggest a shorter skeletal frame size during rearing in pullets under the 4/3 feeding schedule compared to those on the 5/2 schedule, resulting in lighter eggs by hens reared on the 4/3 feeding schedule compared to hens reared on the 5/2 schedule (de Beer and Coon, 2007). Controlling body weight by the end of the rearing phase and managing the flocks the same into the lay phase, de Beer and Coon (2009) also noted that broilers breeders reared ad libitum until 6 wk of age had greater skeletal frame size (larger keels and shanks and higher body ash content) and also laid heavier eggs than pullets under other weekly feed-restricted strategies (daily and non-daily [skip-a-day] feed restriction). Therefore, a slower growth rate during rearing in hens fed non-daily may lead to lighter hatching eggs laid by these hens compared to control hens, potentially due to smaller frame size and slower skeletal development.

Broiler breeder hens lay heavier eggs with age (Hamidu et al., 2007; Iqbal et al., 2016) and egg components (albumen and yolk) are heavier with heavier egg weight (Ho et al., 2011). Broiler breeder hens lay hatching eggs with 50% fat content in the yolk (Lopez and Leeson, 1995; Hester, 2017), and the liver synthesizes and mobilizes yolk lipids under the regulation of sex hormones (Richards et al., 2003; Walzem and Chen, 2014; Hester, 2017). Our results indicate that hens fed the control diet non-daily during rearing laid lighter hatching eggs with a relative heavier yolk than hens fed the control diet daily during rearing. Non-daily feed restriction during rearing has a long-lasting effect on hepatic lipogenesis in broiler breeder hens (de Beer and Coon, 2009), resulting in a higher body fat content compared to hens fed daily during rearing (Vignale et al., 2016). Yolk gets heavier relative to egg weight as hens age (O'Sullivan et al., 1991; Hamidu et al., 2007), and yolk lipid deposition can increase (O'Sullivan et al., 1991; Yadgary et al., 2010) probably due to higher fat retention at later ages (Richards et al., 2003; Chen et al., 2006; Vignale et al., 2016). Thus, hens fed non-daily during rearing might lay eggs with a higher relative yolk weight compared to daily feeding due to metabolic programming associated with high lipogenesis activity leading to higher fatty acid deposition into the yolk (Renema et al., 2001a; van Emous et al., 2015a). Indeed, the heavier yolk weight could compensate for lighter hatching eggs laid by hens fed non-daily during rearing without differences among treatments in live chick weight at hatch. The relative heavier yolk can supply more nutrients for embryo development (van Emous et al., 2015c). In addition, van Emous et al. (2015c) observed no effect of maternal condition on egg weight, egg components, or live chick weight; however, the rearing treatments of hens impacted the (residual) yolk at hatch, suggesting a possible transgenerational effect on the performance of the progeny. Our results suggest that, compared to control hens, hens fed non-daily during rearing laid eggs with a better egg weight uniformity (consistently across age due to better body weight uniformity) that resulted in a better body weight uniformity of their progeny than those from control hens. Literature describing the effect of rearing or maternal condition on (hatching) egg weight uniformity is scarce; however, previous research evaluating the effect of rearing feeding treatments on the proportion of second-grade chicks did not report significant differences (Hocking et al., 2002; van Emous et al., 2015a).

Fertility, Hatchability, and HOF

Fertility, hatchability, and the percentage of HOF have previously been reported to decline with age in feed-restricted broiler breeders (Hocking and Bernard, 2000; van Emous et al., 2015c; Iqbal et al., 2016). Our results show lower hatchability at the end of lay, driven by a decrease in fertility. However, the percentage of HOF followed a cubic curvature with a drop after spiking, especially in control hens. At the time of spiking, 1 overweight male per pen was replaced with 1 young male per pen. Roosters located with hens reared on the control treatment were heavier than the rest, and the heaviest male was likely to be the dominant male with greater access to feeders. The removal of the dominant male may have increased aggressive behaviors to re-establish hierarchy among old and new roosters, taking time away from breeding activity (Hocking and Bernard, 2000; Bilcik and Estevez, 2005). In the case of low breeding activity and fecundity, hens are hypothesized to mobilize "old" sperm stored to fertilize fresh eggs (Hocking and Bernard, 2000), and ovum fertilization with old sperm has been estimated to linearly increase embryo mortality (Lodge et al., 1971). This hypothesis can explain the decline in the percentage of HOF, although the performance of aggressive behavior was not analyzed during lay. Poor reproductive performance, including laying rate, fertility, embryo mortality, and the percentage of HOF eggs, has been reported in heavy broiler breeder hens (Hocking et al., 2002; Renema et al., 2007) due to excessive accumulation of adipose tissue leading to lipotoxicity (Ramachandran, 2014; Walzem and Chen, 2014), in line with our results. Moreover, the body weight of roosters correlated negatively with the percentage of fertility and HOF. Previous studies indicated that male fertility was associated with body weight (Renema et al., 2007; Sarabia Fragoso et al., 2013). Individual body weight variation among males affected fertility and also the percentage of HOF (Lodge et al., 1971). Foot problems or lameness in the roosters can explain the lower fertility associated with heavier males (Carter et al., 1972) but not the low percentage of HOF. The negative effect of excessive body weight of males in the percentage of HOF was probably due to excessive adipose tissue. The effect of rearing treatments on fertility and embryo mortality is hypothesized to be mediated by an indirect effect of body condition at the end of rearing on egg composition (van Emous et al., 2015c).

We found an effect of hen age and feeding frequency during rearing on the proportion of male chicks at hatch, although the sex of dead embryos was not determined. The link between the sex ratio of the progeny and the maternal condition has been previously reported in chickens (Parker, 2002). In the case of poultry, optimal maternal condition is hypothesized to bias the sex ratio of the progeny toward male progeny and poor maternal condition toward female progeny (Aslam and Woelders, 2017). Previous research looking at sex bias indicated that the percentage of male embryos increased in feed-restricted laying hens as egg weight decreased (Aslam et al., 2015), and early embryo mortality was significantly biased toward females in layer strains that laid lighter eggs but not in meat-type strains (Li et al., 2008; Wu et al., 2012). For example, Wu et al. (2012) indicated that 1 meat-type chicken strain biased embryo mortality toward males during late incubation, probably due to larger eggs. Taking this into account, the sex ratio bias at hatch might indicate sex-dependent embryo mortality at the end of lay. Male broiler embryos are more sensitive to incubation temperature (Leksrisompong et al., 2009), which may relate to increasing total embryonic oxygen consumption and total heat production in eggs laid by older broiler breeder hens (Hamidu et al., 2007). Higher heat production from yolk fatty acid oxidation might explain our progeny sex ratio bias at hatch in eggs laid by older hens. Certainly, hens fed non-daily during rearing in our research laid eggs with a relative heavier yolk than hens fed daily during rearing. Therefore, hatching eggs with relative heavier yolk laid by older hens are hypothesized to be at risk for male embryo mortality mediated by endogenous heat production from lipid oxidation. However, this hypothesis does not explain the significantly higher sex ratio of males that hatched from eggs laid by hens fed daily during rearing or the effect of rearing treatment on the percentage of HOF. Therefore, our results might also suggest an effect on primary sex ratio mediated by specific egg components during late lay (Aslam and Woelders, 2017).

CONCLUSION

Our results indicate that rearing treatments affected the flock performance during lay and the feeding motivation of hens at the end of lay. Compared to control hens, hens reared on the 4/3 schedule showed higher feeding motivation at the end of lay and the better body weight uniformity during lay that probably resulted in an improvement in hatching egg weight uniformity and chick weight uniformity at hatch. Roosters housed with control hens showed a faster growth rate compared to roosters allocated to hens on the other 3 treatments, and hens reared on the control treatment had lower feed intake in their home pen at the end of the lay. Laying rate decreased slower during late lay in hens fed the 3 alternative treatments during rearing, and hens reared on the graduated schedule had higher cumulative egg production than control hens. Hatchability decreased earlier during mid lay for eggs laid by control hens compared to those from hens reared on the alternative diet. Additionally, the percentage of male chicks was higher at the end of lay for eggs laid by hens fed daily during rearing compared to those from hens fed non-daily during rearing. In conclusion, rearing feeding treatments impacted the growth rate and body weight uniformity during lay, feeding motivation at the end of lay, and the laying rate and hatchability depending on hens' age.

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