Lifetime productivity of conventionally and precision-fed broiler breeders

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ABSTRACT A precision feeding (PF) system was developed to increase broiler breeder lifetime reproductive performance through improved flock uniformity. The current study consisted of 2 rearing and 3 laying treatments. From 0 to 22 wk of age, 480 Cobb male grandparent line pullets and 80 Cobb MX males were fed once daily as a group (CON), or individually with a PF system. Pullets were housed in 6 replicate pens of 40 birds, and cockerels in one pen per treatment. During lay, CON and PF treatments continued, and a third treatment was added, where PF-reared birds were transitioned to conventional feeding (PFCON; n = 3 pens). At photostimulation (22 wk of age), all pens had 24 hens and 2 roosters. Birds were allowed to mate naturally to 52 wk. Analysis of variance was conducted, and Tukey-adjusted means were reported as different where P < 0.05. Mean BW was near the target BW in all treatments. At photostimulation, PF pullet BW CV was 2% vs 14% in CON pullets. Cumulative feed conversion ratio during rearing was lower in PF treatment pullets, which ate 3% less than CON pullets. Pullets in the PF treatment received 10 meals spread throughout each day, compared with one meal per day in the CON treatment. Increased feeding frequency would reduce diurnal fluctuations in nutrient supply, which may explain why PF pullets had 1.2 times the breast muscle weight of CON pullets at 22 wk. There was no treatment difference in abdominal fatpad weight at 22 wk. The PF treatment had 3.8% higher fertility and 1.3% lower egg weight CV compared with the CON treatment. Egg production in PF and PFCON treatments was 0.73 and 0.89 times that of the CON treatment, respectively. It is hypothesized that metabolic changes in PF pullets provided an insufficient metabolic trigger for sexual maturation. It follows that relaxing feed restriction may increase fat deposition and egg production in PF broiler breeders.

Key words: uniformity, precision livestock feeding, egg production efficiency, sexual maturation, caloric restriction

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INTRODUCTION

Over 50 yr of commercial selection, broiler BW increased over 450% (Zuidhof et al., 2014), but the BW target considered optimal for broiler breeder reproductive efficiency remained virtually constant (Renema et al., 2007b). Thus, the gap between growth potential of broilers and broiler breeder target BW is increasing. The intensity of broiler breeder feed restriction has increased, which creates difficulty for uniform feed distribution and poor flock uniformity. In commercial broiler parent flocks, it is increasingly difficult to distribute the

right amount of feed to each individual bird. Poor BW uniformity may reduce reproductive success because of suboptimal performance in both overweight and underweight birds (Siegel and Dunnington, 1985; Yu et al., 1992a). Nutrient density of feed, the quantity provided, the frequency and timing of feed delivery, feeder design, and feeder space all affect feed distribution, which ultimately influences BW uniformity. Skip-a-day feeding is meant to improve flock BW uniformity by providing an opportunity for the less aggressive birds to compete for a larger amount of feed, although less frequently. Skip-a-day feeding has been criticized from the standpoint of metabolic stress (de Beer et al., 2007), and for welfare reasons related to hunger, frustration, and distress (Mench, 2002). Technologies that ensure rapid and equal feed distribution are reaching their limit, and because of its social responsibility to ensure the welfare of broiler breeders, the hatching egg industry cannot further reduce the frequency of feeding. Either the degree of broiler breeder feed restriction needs to be eased or new feeding technologies to ensure equitable feed distribution are needed or both.

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To achieve high BW uniformity, a precision feeding (**PF**) system was recently developed at the University of Alberta (Zuidhof et al., 2018). The system was designed to weigh free run broiler breeder pullets and hens, and feed an individual bird only if its BW is lower than the target BW. By limiting meal size and duration, it is possible for birds to eat more often than once per day while at the same time achieving a high degree of flock uniformity. The system consistently enables the production of broiler breeder and layer pullet flocks with a BW CV of 2% or less, a previously unprecedented level of flock uniformity (Carneiro, 2016; Zuidhof et al., 2017; van der Klein et al., 2018b). With this sequential PF system, feed-restricted broiler breeders received their daily feed allotment spread over 5 to 12 small meals per day. Feed efficiency increased by 4% compared to conventional daily feeding, most likely due to reduced storage and mobilization of energy and nutrients in the body (Carneiro, 2016).

The objectives of the current study were to compare the flock uniformity of broiler parent stocks raised conventionally and using a PF system, and the resulting impact on lifetime egg production and fertility. Assuming that breeder-recommended target BW profiles are adequate for optimal productivity, the hypothesis was that high flock uniformity in a precision-fed broiler grandparent would increase reproductive efficiency compared with conventionally fed birds, because each bird would respond similarly to photostimulation and feeding cues.

MATERIALS AND METHODS

Experimental Design

The animal protocol was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles established by the Canadian Council on Animal Care Guidelines and Policies (CCAC, 2009). The current study consisted of 2 treatments during rearing, and 3 treatments during laying. The 52-wk study was divided into 2 phases: rearing (0 to 22 wk) and laying (22 to 52 wk). During rearing, the experiment was a completely randomized design with 2 treatments in 6 replicate pens per treatment, each containing 40 pullets: control (CON)—fed conventionally, once per day, as a group; and PF—fed using a precision feeding station. During lay, there were 3 experimental treatments in a completely randomized unbalanced design: CON-fed conventionally, once per day, as a group (n = 6 pens)of 24 hens and 2 roosters); PF—fed by a PF station (n = 6 pens of 24 hens and 2 roosters); and a third treatment where some birds that had been reared on PF were fed conventionally, once per day, as a group (**PFCON**; n = 3 pens of 24 hens and 2 roosters). The laying phase was divided into 2 periods. From 23 to 42 wk of age, identical breeder-recommended target BW were used. By 43 wk of age, egg production results and individual feed intake data suggested that some PF hens had not commenced laying. Therefore, the target BW in the PF treatment only was increased by 400 g to determine whether an additional metabolic signal would stimulate the onset of egg production in the PF treatment. Thus, during the period from 43 to 52 wk of age, the target BW of the PF treatment was higher than the CON and PFCON treatments. The pen was the experimental unit for CV, feed intake, efficiency, and egg production analyses. For BW and carcass analyses, individual birds were the experimental unit, and pen was a random effect. During rearing, the males were randomly assigned to 1 of 2 replicate groups to calculate BW CV, and each of these replicates was considered an experimental unit for CV analysis.

Stocks and Management

Diets Using a commercial phase feeding program, identical feeds were provided to all treatments throughout the study. Commercial broiler breeder diets were fed as follows: starter (2900 AME, 19% CP, 1.1% Ca) from 0 to 3 wk of age; developer (2589 AME, 14.2% CP, and 0.9% Ca) from 3 to 23 wk of age; and 2 laying diet phases: peak layer diet (2689 AME, 15.0% CP, and 3.3% Ca) from 23 to 35 wk of age; and post peak layer diet (2682 AME 14.6% CP, and 3.3% Ca) from 35 to 52 wk of age.

Rearing Phase A total of 480 Cobb grandparent females and 80 Cobb MX males were used in the study. This male line female grandparent (**GP**) was chosen because uniformity is difficult to achieve with this line. Upon delivery from the hatchery, 40 pullets were assigned randomly to each of 6 replicate pens per treatment. An additional 80 cockerels were randomly assigned to 1 of 2 additional pens (40 per pen) for conventional or precision feeding. This conditioned the males to the treatment-specific feeding systems that they would use during the laying period. At the start of the rearing phase, stocking pressure was 6.5 birds/m^2 $(1.65 \text{ ft}^2/\text{bird})$. The rearing photoschedule was 23L:1D for the first 3 d after placement (25 lx), and then maintained at 8L:16D (8 lx) until photostimulation at 22 wk of age.

Laying phase At 22 wk of age, the photoperiod was increased to 14L:10D (25 lx). All birds were redistributed into 15 pens for the laying phase. Twentyfour females were placed with 2 males in all pens, with a male: female ratio of 1:12. The stocking pressure after 22 wk of age was 4.2 birds/m² (2.5 ft²/bird). To maintain approximate breeding ratios, a separate pen of replacement males was maintained; males were replaced when culled or dead. Dead or culled females were not replaced. At 43 wk of age, it was apparent that some PF hens had not commenced laying, so the target BW in the PF treatment was increased by 400 g to determine whether an additional metabolic signal would stimulate the onset of egg production in the PF treatment.

PRECISION-FED BROILER BREEDERS

Description	Training mode	Training mode with door movement	Individual feeding mode
Individual feed access	No	No	Yes
RFID tags read	No	No	Yes
Individual BW	No	No	Yes
Ejector activation	No	Yes	Yes
Entry door open/close Feed disappearance recorded	No Yes (for all birds as a group)	Yes (remain open for several minutes) Yes (for all birds as a group)	Yes (closes after individual bird entry) Yes (for individual birds)



Figure 1. Feeding chamber of a precision feeding station shown during training period (prior to 8 d of age). Supplemental feed was provided on a paper plate on the floor of the feeding chamber from 0 to 7 of age. The wall of the station on the left shows the feeder access, picturing a chick with its head in the feeder. The feeder width was restricted for chicks to prevent them entering the feeder.

Precision Feeding Precision feeding started with a 14 d training phase. The feeding stations were programmed with a training mode such that the entry doors were open continuously (see Table 1). During training mode, the feeder was checked every 5 min for feed disappearance (consumed or wasted), and topped up if it contained less than the target amount of feed. At day 0, approximately 40 g of supplemental feed per bird was divided onto paper plates placed near the PF station ramp and inside the station (Figure 1). Feed was also placed on the ramp so that birds could follow a trail of feed into the feeding station. After 2 d, feed was only placed on the ramp and inside the feeding station. After 7 d, the birds ate only from the feeder inside the PF stations. From 7 to 14 d of age, a modified training mode was implemented to familiarize the birds with the sounds and movements of the feeding station (Table 1). Every 15 min, the entry doors would close, and all birds inside the station were gently ejected. The feeder topped up, and the cycle repeated. At 14 d of age, individual feeding commenced. In this mode, the entry door would close after an individual bird entered the station and its BW was recorded. The BW was compared with a target BW, and if the BW was less than the target BW the bird would receive access to feed for a short period of time, after which it was ejected. If its BW was greater than the target BW, it was immediately ejected without being provided access to feed. The feeding bout duration and quantity of feed available to the birds throughout the experiment is summarized in Table 2.

Remedial Training During the week of transition to individual feeding, 88 out of 280 pullets and cockerels (31%) did not immediately adapt to the system. It was possible to identify these birds because they had no or few feeding events registered to their radio frequency identification (RFID) tags in the PF system database. Birds not eating for more than 24 h were placed

Table 2. Precision feeding system software settings used to control the duration of each feeding $bout^1$ and the quantity of feed presented to the pullets in the feeder.

Phase	Age, d	Duration, s	Quantity, g
Training ²	0 to 13	300	70
Rearing	14 to 20	45	70
Ũ	21 to 22	45	45
	23 to 37	45	25
	38 to 154	45	12
Laying	155 to 200	45	12
	200 to 364	45	20

 $^1\mathrm{Time}$ birds were allowed to eat prior to being gently ejected from the feeding station

²Birds were not ejected from the feeding station. Feed disappearance was determined after every feeding bout prior to the feed being replenished.

together in a PF pen identical to their own for a remedial training period. The PF station was placed in training mode initially to entice the birds to eat freely as a group from the feeder. The training mode served as a reminder to the birds that the PF station was their source of food. After 30 min, individual feeding was initiated. Perhaps due to a change in the social hierarchy, 60% of birds in the remedial PF pen required only a single brief (1 to 24 h) training bout to complete their training. Birds were returned to their original pens once feed was detected in their crop by palpation. The lowest BW birds tended to need the most remedial training. A total of 14 of the remedially trained birds had particularly low BW, and were finally returned to their original pens at day 23, at which time their average BW (374 g) was 67% of the birds that did not require remedial training (555 g).

Thereafter, individual feeding was based on the BW of individual birds relative to their target BW. Birds were weighed upon every visit to the PF station. If their BW was above the target BW, they were immediately ejected from the feeding station. If their BW was below the target BW, they received access to a small amount of feed for a short feeding bout (45 s; Table 2), prior to being gently ejected from the station. The bout duration and feed quantities were chosen to first encourage birds to eat from the feeder, and subsequently to prevent them from eating their entire allocation for the day in 1 bout. Using this approach, birds typically received an average of 10 small meals over 60 visits per 24 h period (Table 3). The PF stations were equipped with green LED lights, mounted in the entry doors and the feeder, at an intensity of 15 lx. The color and intensity of this supplemental light were intended to allow birds to see well enough to use the stations during the scotophase without stimulating hypothalamic photoreceptors (Rodriguez, 2017).

Body Weight and Feed Intake During the training period (from 0 to 14 d of age), all PF birds were individually weighed daily to determine if they were accessing feed and growing. During this period, the CON chicks were weighed every second day to enable comparison of growth trajectories during the first 2 wk. After transition of the PF treatment to individual feeding, the number of visits to the PF stations ranged from 28 to 138 visits per pullet per day (Table 3). Median BW for each individual bird were determined from database records of all visits to the feeding station. Feed intake was calculated for every feeding bout by subtracting the final feeder weight from the initial feeder weight, and summed daily for each individual bird.

In the CON treatment, weekly individual BW were recorded from 4 to 35 wk of age to calculate the BW CV and to calculate the mean BW for use in the feed allocation decisions. After peak production (36 to 52 wk) individual BW were recorded biweekly. Feed allocations were adjusted to achieve the breeder-recommended target BW. Because microclimate conditions such as temperature and lighting vary slightly from pen to pen, a unique per-bird feed allocation was estimated for each pen. For the CON treatment, 3 pan feeders with 33 cm diameter provided 8 cm/bird of feeder space in the CON pens. At 6 wk of age, a fourth pan feeder was added, increasing the feeder space to 11 cm/bird. During lay, females were provided with 2 female feeders with restriction grills to exclude males (9 cm/hen); males were provided 50 cm of feeding space per rooster from a single male pan feeder. After photostimulation, male feeders were elevated so that hens could not steal their feed.

Carcass Development

At 16 wk of age, 25 females and 16 males per feeding treatment were dissected to evaluate carcass development. These birds were euthanized by cervical dislocation prior to the CON birds being fed. At 22 wk of age, an additional 8 pullets per feeding treatment (no roosters) were euthanized approximately 8 h after the CON birds were fed, and dissected to determine whether the feeding system treatments caused any developmental differences. At 52 wk of age, 18 females per feeding treatment, and all the males (n = 12 for the PF and CON treatment, and n = 6 for the PFCON treatment) were dissected.

Egg Production and Fertility

At 16 wk of age, nest boxes were introduced to each pen so that pullets could familiarize with the nests. Eggs were collected at least 2 times daily, and the number of eggs produced in each pen was recorded. Egg weights were recorded on all eggs produced 1 d/wk and uniformity of egg size was calculated. Beginning at 30 wk of age, eggs were incubated for 7 d, after which fertility was assessed by candling and breakout. At the end of lay, birds were categorized into those that were laying or not, based on the presence of large yellow follicles (**LYF**) on the ovary. These 2 categories were used to investigate differences in body composition at the end of lay.

Table 3. Simple statistics¹ summarizing feeding behavior of precision-fed Cobb grandparent pullets from 2 to 22 wk of age.

	Mean	Min	Max	Range	SD	CV (%)
Visits, #/d	61	28	138	110	16	25
Meals, #/d	10	2	44	42	4	44
Visits without meals, #/d	51	22	132	110	17	33
Success ratio, meals: visits	17%	4%	63%	59%	9%	54
Meal size, g/meal	7.7	1.0	19.1	18.2	2.5	32

¹Simple statistics were calculated from weekly individual bird averages from 2 to 22 wk of age.

Statistical Analysis

One- and 2-way ANOVA were conducted using the MIXED procedure of SAS (Version 9.4, SAS Institute Inc., Cary, NC, 2012) on all data to determine the effect of treatment and age, treatment and sex, or laying status on the measured parameters. Each pen was considered an experimental unit for CV, feed intake, efficiency, and egg production analyses. For BW and carcass analysis, individual birds were considered the experimental unit, and pen was considered a random effect, and BW was included as a covariate. Tukey's range test was applied to multiple mean comparisons to reduce type II errors (false positives). Differences between means were reported as significant where P < 0.05. Trends were reported where P < 0.1.

RESULTS AND DISCUSSION

Individual Precision Feeding Behaviour

Simple statistics describing feeding behavior patterns in the PF treatment for the rearing period are presented in Table 3. The average number of PF station visits ranged from 28 to 138 visits per bird per day. This type of individual variation in feed seeking behavior is common in our PF trials, and reflects differences in individual bird temperament. From 2 to 22 wk of age, birds visited the feeding stations an average of 61 times per day, eating an average of 10 meals per day. The number of visits to the PF station that did not result in a meal averaged 51 per day, which is equivalent to a 17% success ratio (Table 3). Meal sizes ranged from 1 to 19 g, with a mean of approximately 8 g. There was a high degree of variability in feed seeking and feeding behavior. The CV of weekly means for individual birds ranged from 25% for the number of visits per day to 54% for the meal: visit ratio.

Body Weight, Gain, and Uniformity

Brooding Phase (d 0 to 14) The brooding period corresponded to a training period for the PF chicks, during which time they learned to visit the PF stations to find feed, as described in the methodology section. During this period, the CON pullets and cockerels

gained BW consistently in a mostly unconstrained sigmoidal manner. In contrast, PF chicks showed evidence of constrained growth beginning at day 8 (see Figure 2). After day 7, supplemental feeding travs were removed from the PF stations (see Figure 1), and birds had access to feed only from the PF station feeder, which measured 10 cm in length and provided 0.25 cm of feeder space per bird. Thus, low PF feeder space during the second week was likely the reason why males and females in the PF treatment showed a slower BW increase compared with the CON treatment (Figure 3), and an increase in BW CV compared to the CON birds at 2 wk of age (Figure 4). During subsequent time periods, PF treatment birds were fed one at a time in a sequential manner, providing the full 10 cm of feeder space per bird.

Rearing Phase (wk 2 to 22) Immediately after the start of individual feeding in the PF treatment on day 14, BW CV decreased rapidly (Figure 4), reaching 3.5% vs. 11.4% in the CON treatment by 6 wk of age, and 0.8% vs. 12.7% in the CON treatment by 11 wk of age. At 21 wk of age, pullet BW CV was 1.4% in the PF treatment compared with 13.8% in the CON treatment. Lower BW PF pullets and cockerels were able to catch up to larger pen mates that were constrained to a slower rate of growth by the upper BW limit imposed by the PF system. Body weights closely followed the breeder-recommended target BW (Figure 3). From 2 to 22 wk of age the BW gain of the CON treatment pullets (16.5 g/d) was lower compared with 17.6 g/d in the PF treatment (Table 4). The difference in ADG was partly due to the PF pullets having lower BW than the CON birds when they transitioned to individual feeding at 14 d of age, and partly because the PF pullets were 95 g heavier than the CON treatment at 21 wk of age. Pullets in the PF treatment had a higher week 3 and 4 ADG compared with the CON treatment, immediately after individual feeding began. Average daily gain fluctuated more from week to week in the CON treatment compared to the PF treatment (Figure 5). This was because the PF system adjusted feed intake in real time to compensate for changes in nutritional requirements that might have occurred due to factors such as, but not limited to, microclimate temperature and light intensity, feed composition, immune challenges, and activity. The ADG of CON treatment pullets at 17 wk was lower compared with the PF treatment (Figure 5) due to underestimation of the feed allocation needed by



Figure 2. Body weights of individual Cobb grandparent pullets (top row) and Cobb MX cockerels (bottom row) during the brooding period for conventionally fed (CON; left column) and precision-fed (PF; right column). During the brooding period, all chicks were fed ad libitum and PF chicks were familiarized with the PF system (training period).

the CON treatment pullets at this age. Thus, at 21 wk of age, BW of the PF treatment was 99.0% of the target BW, compared with 95.3% in the CON treatment (Figure 3). Figure 6 shows a composite plot of the BW of each individual bird during the entire study, illustrating excellent control of BW in the PF treatment in both the males and the females.

Laying Phase (wk 22 to 52) There was no effect of treatment on ADG during the laying phase (Table 4). Similar to the rearing phase, the rate of gain from week to week was steadier in the PF hens compared with the CON and PFCON treatment hens (Figure 5). This reflects the fact that feed allocations in the PF treatment were done in real time by the PF



Figure 3. Body weights of Cobb grandparent females (A) and Cobb MX males (B) conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON). Hens in the PF treatment only were stimulated with an abrupt target BW increase of 400 g. Target BW and the adjusted target used to stimulate PF hens at 43 wk of age (PF stimulate) are shown for reference. ^{a,b}Means within age with no common superscript differ significantly (P < 0.05).

system, in contrast with the less sensitive weekly and biweekly intervals for CON feed allocation decisions. After 43 wk of age, there was an abrupt increase in ADG (Figure 5) and BW (Figure 3) in the PF treatment in response to an increase in the PF target BW intended to stimulate sexual maturation in that treatment. In the PFCON treatment, where birds transitioned from the PF treatment during rearing to the CON treatment during the laying phase, hen BW CV increased from 3.5% at 23 wk of age to 12.6% by 30 wk, and more slowly thereafter to 14.7% by 52 wk of age (Figure 4). From 30 wk of age onward, the PF-CON BW CV was significantly greater than in the CON treatment, which had a BW CV of 11.3% at 52 wk. A similar trend was observed in the males, but with greater variability from week to week compared with PFCON females, likely due to sample size. After spiking CON treatment males at 45 wk of age, which were quite variable in BW, the BW CV dropped to a level not significantly different from the PF males (Figure 4). The PF males were remarkably uniform (see Figure 6), ending the study with a BW CV of 0.22%, compared with 15% in the PFCON treatment. At 52 wk of age, the CON treatment BW CV (6.6%)was not different from the PF or PFCON treatments (Figure 4).

Feed Intake

Rearing Phase Cumulative feed intake for pullets from 2 to 22 wk of age was 160 g higher in the CON treatment (8.29 kg) compared with the PF treatment (8.36 kg; Table 4). Feed intake in the PF treatment varied more from week to week compared with the CON treatment (Figure 7) because the PF system allowed real-time adjustment of feed intake in response to environmental factors impacting nutrient requirements and any feed variability that may have impacted nutrient intake. Conversely, feed allocation decisions for the CON treatment were based on past and anticipated growth rates, with less than perfect knowledge of dietary nutrient levels, previous and future physiological state, microclimate conditions, and health status. Notably, the SEM for cumulative feed intake was higher for the PF compared with the CON treatment, due to real-time feed intake adjustments in the PF treatment.

From 16 to 20 wk of age, feed allocation decisions for the CON treatment pullets were too conservative, delaying the desired accelerated pre-pubertal BW increase for the CON pullets compared with the PF pullets (Figure 3). As a result, CON pullet BW was on average 94 g behind the PF pullets from 17 to 21 wk. Because there was only 1 experimental unit for



Figure 4. Coefficient of variation for BW of Cobb grandparent females (A) and Cobb MX males (B) conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON). ^{a-c}Means within age with no common superscript differ significantly (P < 0.05).

the CON males during rearing, no statistical analysis of feed intake was conducted during the rearing phase. However, in spite of a greater numerical difference in cumulative feed intake than observed in the females (Table 4), growth of the PF males was very similar to the CON males (Figure 3B).

Laying Phase From 22 to 52 wk of age, average daily feed intake (**ADFI**) of CON and PFCON treatment hens was higher compared with the PF treatment hens; cumulative feed intake was 3.4 kg higher in the CON treatment compared with the PF treatment

(Table 4). Feed intake in the PF treatment increased after the increase in the PF treatment hen target BW at 43 wk (Figure 7), but remained lower than the CON and PFCON treatment hens. Average daily feed intake was higher in the CON roosters (110.8 g/d) compared with the PFCON treatment roosters (103.8 g/d), which also had significantly greater ADFI compared with the PF treatment roosters (98.4 g/d; Table 4). If the CON and PFCON roosters were able to steal feed from the female feeders, this did not show up as a reduction in ADFI compared with the PF treatment, where it was **Table 4.** Average daily feed intake (ADFI), average daily gain (ADG), and cumulative¹ feed intake, and feed conversion ratio (FCR) of Cobb grandparent females and Cobb MX males conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON).

			Treatment (T)						Source of variation		
Variable	Sex	CON	SEM	PF	SEM	PFCON	SEM	Т	Age (A)	ТхА	
Rearing phase (2 to 22 wk)									- Prob $>$ F $-$		
ADG, g/d	F	16.5^{b}	0.2	$17.6^{\rm a}$	0.2			< 0.001	< 0.001	< 0.001	
ADFI, g/d		61.2	0.1	61.8	0.3			0.10	< 0.001	< 0.001	
Cumulative feed intake, kg		8.29^{a}	0.01	8.36^{b}	0.03			< 0.001	< 0.001	< 0.001	
Cumulative FCR, g:g		$3.894^{\rm a}$	0.018	3.720^{b}	0.035			< 0.001	< 0.001	< 0.001	
ADG, g/d	M^2	19.5		20.1				_	_	_	
ADFI, g/d		64.4		60.3				_	_	-	
Cumulative feed intake, kg		8.90		8.60				_	_	-	
Cumulative FCR, g:g		3.748		3.307				_	_	-	
Laying phase $(22 \text{ to } 52 \text{ wk})$									$- \operatorname{Prob} > F -$		
ADG, g/d	F	10.0	0.4	10.3	0.4	11.3	0.6	0.23	< 0.001	< 0.001	
ADFI, g/d		$143.5^{\rm a}$	0.3	127.6^{b}	0.8	$143.4^{\rm a}$	0.9	< 0.001	< 0.001	< 0.001	
Cumulative feed intake, kg		29.97^{a}	0.12	26.57^{b}	0.25	29.62^{a}	0.56	< 0.001	< 0.001	< 0.001	
ADG, g/d	Μ	8.4	0.9	7.9	0.9	10.1	1.3	0.38	< 0.001	< 0.001	
ADFI, g/d		110.8^{a}	0.7	98.4°	1.4	103.8^{b}	1.1	< 0.001	0.022	0.87	
Cumulative feed intake, kg		$22.54^{\rm a}$	0.26	20.00^{b}	0.57	$21.01^{a,b}$	0.46	< 0.001	< 0.001	0.24	
Cumulative FCR, g:g		$16.004^{\rm a}$	0.931	15.264^{a}	0.606	12.035^{b}	0.313	< 0.001	< 0.001	0.62	

¹Cumulative means are reported at the end of the rearing and laying phases.

²Due to practical limitations, males for the PF and CON treatments were reared in a single pen, then distributed to the female pens at 22 wk of age for the purpose of natural mating. Therefore, simple means are reported for males during the rearing phase.

^{a-c}Means within row with no common superscript differ significantly (P < 0.05).



Figure 5. Average daily gain of Cobb grandparent females conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON). Target BW gain and the adjusted target used to stimulate PF hens at 43 wk of age (PF stimulate) are shown for reference. ^{a-c}Means within age with no common superscript differ significantly (P < 0.05).

impossible for the males to steal from the females because the PF stations fed individual birds in a protected area, and recorded all feed intake events. Cumulative feed intake for the roosters followed the same trends as ADFI, but was not significantly different at 52 wk of age.

Feed Efficiency

For the rearing period, cumulative pullet feed conversion ratio (**FCR**) in the PF treatment was 0.96 of the CON treatment (3.72 vs. 3.89 g: g, respectively). This is consistent with previous observations where from 10



Figure 6. Body weights of individual Cobb grandparent females (top row) and Cobb MX males (bottom row) conventionally fed (CON, left column) and precision-fed (PF, right column), illustrating the high degree of BW uniformity achieved with precision feeding.

to 23 wk of age, precision-fed Ross 308 broiler breeders were 3.9% more efficient than skip-a-day fed counterparts (Carneiro, 2016). In the PF treatment, efficiency may have increased by more frequent feeding, allowing birds to utilize nutrients directly from the gastrointestinal tract, and reducing the need to store nutrients in the body and mobilize them later. In contrast, the CON birds, which were fed only once per day, experienced much more dramatic diurnal swings in energy balance. They were likely conditioned to store energy and nutrients in the hours immediately after feeding and mobilize them during a period of negative energy balance after depleting the digesta of nutrients. According to the laws of thermodynamics, storage and mobilization of nutrients cannot be a 100% efficient process. An analogous efficiency improvement related to feeding frequency was reported by Zuidhof et al. (2015) in daily vs. skip-a-day fed pullets. Converting nutrients and energy to a suitable storage form and mobilizing to regenerate a useable form during fasting is a source of additional heat production when feeding frequency is reduced, such as in the CON treatment of the current study.

During the laying phase, males in the PFCON treatment had a lower FCR (12.035) compared with the CON and PF treatments (16.004 and 15.264 g: g, respectively; Table 4). This was not because of lower ADFI in the PFCON treatment, but rather due to a greater increase in BW compared with the PF and CON treatment roosters, particularly after 36 wk of age (Figure 3B). Based on the observation that PFCON

roosters had lower ADFI than the CON treatment roosters, yet had a substantial improvement in feed efficiency, it may be possible that the PFCON treatment roosters stole more feed from the female feeders. As discussed previously, ADFI in the PFCON treatment roosters was greater than in the PF treatment roosters; however, it was also significantly lower than in the CON treatment. Given the relatively large increase in PFCON BW while consuming less feed than the CON treatment, it cannot be ruled out that the apparent efficiency was realized because PFCON males were stealing more feed than CON treatment males. The low SEM in PFCON FCR raises some doubt about this hypothesis, because such a low SEM implies uniform feed stealing behavior from pen to pen. It is possible that rearing feeding treatment could have a predisposing effect on feed stealing during the laying phase, but this conclusion is hypothetical, and cannot be deduced from the current data.

Reproductive Performance

Egg Production Cumulative egg production per hen to 52 wk of age was highest in the CON treatment (89.1 eggs), compared with 71.3 eggs in the PF-CON treatment and 64.9 eggs per hen in the PF treatment (Table 5). These are lower than commercial broiler breeder numbers and reflect the fact that these were male line grandparent hens. Hen day egg production (Figure 8) was consistently higher in the CON treatment compared with the PF and PFCON treatments,



Figure 7. Average daily feed intake of Cobb grandparent females (A) and Cobb MX males (B) conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON). ^{a,b}Means within age with no common superscript differ significantly (P < 0.05).

from earlier onset of lay to persistency (Figure 8). The PF treatment hens laid 73% of the number of eggs laid by CON hens. The attempt to stimulate egg production in the PF treatment by increasing target BW after 43 wk of age did appear to increase egg production beginning at 45 wk of age (Figure 8). Several tiny eggs with no yolks were recovered from the PF treatment at this time, which were similar to what is often observed at the onset of laying, which suggested that some birds were stimulated into production by the 43 wk metabolic cue. In another study using Ross 308 broiler breeders, egg production in precision-fed hens was only 84% of skip-a-day fed hens (P < 0.001; Zuidhof, unpublished data). Testing the impact of increased BW on egg production of precision-fed Ross 708 hens, van der Klein et al. (2018a) reported that a 22% increase in target BW over the breeder-recommended target BW corrected this problem. Hens at the breeder-recommended BW laid only 72% as many eggs as the high BW treatment to 55 wk of age. The optimal BW for precision-fed hens remains to be determined, but it would appear that the metabolic changes due to feeding frequency will require higher target BW for reproductive success in precision-fed hens.



Figure 8. Hen-day egg production of Cobb grandparent females conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON). ^{a,b}Means within age with no common superscript differ significantly (P < 0.05).

Significant relationships between carcass traits and hen reproductive status were observed at the end of the laying period (Table 6). The percentage of hens in lay at 52 wk of age was 67, 44, and 72% in the CON, PF, and PFCON treatments, respectively (P = 0.27). Birds in lay at 52 wk of age had on average 4.9 LYF, and this did not differ between treatments (data not shown). Hens in lay had 1.25 times the liver weight of those not in lay, which would be expected since the liver is the site of vitellogenin synthesis (Deeley et al., 1975; Johnson, 2000). Hens that were not in lay had 1.07 times the breast muscle and 0.46 times the fatpad weight compared with hens that were in lay, as a percentage of live BW (Table 6).

Egg Mass Egg weight (Figure 9) was inversely related to egg production (Figure 8). Thus, the PF treatment had the highest egg weight, the CON

treatment had the lowest egg weight, and the PFCON treatment was intermediate (Table 5). Overall egg mass (Figure 9) was highest in the CON treatment because of the significantly higher egg production in that treatment (Table 5). Hens in the PF and PFCON treatments, which were precision fed during rearing and had very low BW variability at photostimulation, produced eggs with more consistent weights compared with CON treatment hens (8.1 and 7.5, vs. 9.4% CV, respectively; Table 5).

Fertility Fertility in the PF and PFCON treatments (90.9 and 89.8%, respectively) was higher than in the CON treatment (87.1%; Table 5). There was a treatment \times age interaction for fertility due primarily to a drop in fertility in the CON treatment around 42 wk of age as male uniformity decreased (Figure 6). After spiking at 45 wk of age in the CON treatment, fertility

Table 5. Egg production, fertility, egg weight, egg weight CV, and egg mass of Cobb grandparent females conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON).

Treatment (T)	Eggs	SEM	Egg weight	SEM	Egg Mass	SEM	Egg weight CV	SEM	Fertility	SEM
	To	tal ——	g -		g/c	l	—— % —		——% of	set ——
CON	89.1^{a}	3.1	58.9°	0.13	27.9 ^a	0.6	9.4^{a}	0.3	87.1^{b}	0.9
\mathbf{PF}	64.9^{c}	5.4	$62.0^{\rm a}$	0.18	21.0^{b}	0.5	8.1^{b}	0.3	90.9^{a}	0.6
PFCON	71.3^{b}	4.8	60.4^{b}	0.23	22.8^{b}	0.8	7.5^{b}	0.3	89.7^{a}	0.8
Source					Pr	ob > F —				
Т	< 0.	.001	< 0.00)1	< 0.0	01	< 0.001		< 0.0	01
Age (A)	< 0.	.001	< 0.00)1	< 0.0	01	< 0.001		< 0.0	01
ΤxΑ	< 0.	.001	0.14	0.14		16	0.29		< 0.001	

^{a-c}Means within column with no common superscript differ significantly (P < 0.05).



Figure 9. Egg weight and egg mass of conventionally fed (CON), precision-fed (PF), and conventionally fed hens reared on the PF system (PFCON).

increased to a level that was not significantly different from the PF and PFCON treatments. Fertility in the PF and PFCON treatments was consistently higher than in the CON treatment from 33 to 46 wk of age. Since uniformity was poor in the PFCON males and females (Figure 4), lifetime fertility may depend on a combination of male and female uniformity and body composition at the time of photostimulation. Bilgili and Renden (1985) reported a negative correlation between total whole body fat and all fertility traits measured. The PF-reared pullets (thus PF and PFCON hens) had a 20% larger breast muscle at photostimulation

Laying (L)	LYF	SEM	Liver	SEM	Breast	SEM	Fatpad	SEM
	Nun	nber ——		g		% of li	ive BW ———	
No	0.00^{b}	0.24	77.2 ^b	5.1	28.01^{a}	0.57	0.77^{b}	0.23
Yes	4.90^{a}	0.20	96.2^{a}	3.7	26.21^{b}	0.46	1.69^{a}	0.18
				F	Prob > F ———			
	< 0.	.001	0.0	005	0.0	18	0.00)3

Table 6. Relationship between laying status¹ at 52 wk of age and the number of large yellow follicles (LYF), liver weight, and percentage of breast and abdominal fatpad of Cobb grandparent females.

¹Percentage of hens in lay at 52 wk of age was 67, 44, and 72% in the conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON) treatments (P = 0.27).

^{a,b}Means within column with no common superscript differ significantly (P < 0.05).

compared with the CON treatment pullets, which may have also contributed to higher fertility.

Carcass Traits

Sex Effects There were several sex effects on carcass composition at 16 and 52 wk of age that although interesting, were not the primary focus of the study. For example, at 16 wk of age, males had 0.83 of the proportional breast muscle weight of females (Table 7). Although it is counterintuitive because their BW and breast muscles tend to be smaller on an absolute basis, female broilers consistently demonstrate a higher proportional breast yield compared with males (Young et al., 2001; Zuidhof, 2005; Zuidhof et al., 2014; van der Klein et al., 2016). This intrinsic sex difference in combination with the fact that the pullets in the current study were a male line GP explains the substantial sex difference in proportional breast muscle weight. At 52 wk of age, rooster liver and breast weights were approximately 75% of females. Rooster fatpad weight at 52 wk of age was remarkably low—only 0.016% of live BW, and only 1.2% of the fatpad weight of females at the end of lay.

Treatment Effects There were no treatment differences in BW in birds dissected for composition analysis (Table 7). At 16 wk of age, liver weight was greater in the PF treatment compared with the CON treatment (30.0 vs. 26.8 g, respectively; Table 7). In the 24 h prior to dissection the CON and PF treatment birds had consumed a similar amount of feed; however, at the time of dissection, birds in the CON treatment had been without feed for 24 h, while the PF treatment birds had been consuming their daily allocation spread over the same 24 h timeframe (see Table 3). Liver weight has a dramatic temporal response to feed intake (de Beer et al., 2007), which provides the most likely explanation for the treatment difference in 16-wk liver weight observed in the current study. At 16 wk, there was a trend toward abdominal fatpad in the CON treatment being 1.7 times the proportion of abdominal fatpad in the PF treatment pullets (P = 0.08; Table 7).

At 22 wk of age, liver weight was significantly greater in the CON treatment compared with the PF treatment (Table 7). This change from the 16-wk observation was likely due to a difference in the timing of feeding relative to the time dissection. At 22 wk of age, the CON birds were fed 8 h prior to dissection, compared with 24 h at week 16. de Beer et al. (2007)found approximately a 10% increase in relative liver weight 8 h after feeding daily-fed pullets, which is similar to the difference observed in liver weight between the PF and CON pullets. The difference in timing of feeding relative to dissection at 16 and 22 wk provide a rational explanation for the otherwise contradictory finding at the 2 ages. At 22 wk of age, the proportional breast muscle weight of PF pullets was 1.2 times that of pullets in the CON treatment (Table 7), although no treatment difference was observed in proportional fatpad weight. This dramatic difference was due in part to a difference in gut fill, which added approximately 168 g to the BW of the CON pullets; however, the absolute breast weights of the PF pullets at 22 wk were also 1.19 times that of the CON pullets (data not shown).

The observation that at the same mean BW, PF pullets had 1.2 times the breast muscle of CON pullets at photostimulation stands in sharp contrast with the conclusion of Eitan et al. (2014) that threshold lean body mass (rather than body fat content) determines the onset of maturation. It is possible that there may be multiple thresholds required for the onset of lay. The hypothesis that metabolic factors may activate the broiler breeder hypothalamic-pituitary-gonadal axis (Bedecarrats et al., 2016) is consistent with the results of the current and recent PF studies, and with the observation that nutrient intake limiting BW gains during sexual maturation delayed sexual development (Renema et al., 2007a). However, the PFCON hens also had only 80%of the egg production compared with the CON hens. The PFCON hens were fed once per day, and therefore had very similar diurnal fluctuations in energy balance. Still, they underperformed the CON treatment. van der Klein et al. (2018b) observed, possibly for the first time, that 19% of PF-fed hens on the breeder-recommended BW profile did not reach sexual maturity, whereas all birds grown 22% heavier by 21 wk of age laid eggs. Similarly, 16% of PF birds that were challenged in some way, either grown precisely to a lower (breederrecommended) BW or photostimulated at 18 wk of age, did not reach sexual maturity to 55 wk of age, whereas all high BW PF hens photostimulated at 21 wk of age did lay eggs (van der Klein et al., 2018a). This suggests

PRECISION-FED BROILER BREEDERS

Age	Effect	BW	SEM	Liver	SEM	Breast	SEM	Fatpad	SEM
16 wk	Treatment (T)		;	g		% of live BW			
	CON	1904	42	$26.8^{\rm b}$	2.8	18.85	0.17	0.104	0.073
	\mathbf{PF}	1941	5	30.0^{a}	3.3	18.65	0.22	0.061	0.088
	Sex(S)								
	F	$1,731^{\rm b}$	25	28.9	2.1	$20.54^{\rm a}$	0.24	0.149	0.056
	М	2.114^{a}	34	27.9	4.1	16.95^{b}	0.25	0.016	0.107
	BW^1	-	_	13.3	4.0	2.5	0.8	0.34	0.08
Source of variation					Pro	b > F —			
	Т	0.3	38	0.0)22	0.4	7	0.08	83
	S	< 0.	001	0.	69	< 0.0	001	0.1	.0
	ΤxS	0.8	31	0.	98	0.3	1	0.0	77
	$_{\rm BW}$	-		0.0	002	0.00)4	<0.0	001
22 wk	Treatment			r			% of li	ve BW ——	
	CON	2880	111	, 52.2 ^a	3.2	21.78^{b}	0.59	0.636	0.071
	PF	2643	13	41.6 ^b	2.3	26.17 ^a	0.53	0.849	0.150
	BW	-	-	19.8	10.2	4.46	1.86	1.37	0.22
Source of variation									
	Т	0.0	71	0.0)36	< 0.0	001	0.24	
	$_{\rm BW}$	-		0.	10	0.05	52	< 0.001	
52 wk	Treatment (T)		ş	g			—— % of li	ve BW ——	
	CON	4406	89	90.1 ^a	2.7	22.97	0.41	0.675	0.127
	\mathbf{PF}	4421	27	67.6°	3.5	24.33	0.54	0.703	0.125
	PFCON	4520	147	77.7^{b}	3.0	23.18	0.40	0.623	0.132
	Sex(S)								
	F	4348	65	89.6^{a}	2.8	27.01^{a}	0.37	1.318^{a}	0.148
	Μ	4550	96	$67.4^{\rm b}$	2.3	19.98^{b}	0.39	0.016^{b}	0.009
	$_{\rm BW}$	-	-	19.6	3.2	-0.61	0.63	-0.006	0.004
Source of variation				P		Prob > F			
	Т	0.8	30	< 0.001		0.14		0.91	
	S	0.1	11	< 0.	.001	< 0.0	001	< 0.0	001
	ΤxS	0.0)57	0.	007	0.2	24	0.9	95
	$_{\rm BW}$	-		< 0.	.001	0.3	34	0.1	11

Table 7. Body conformation 16, 22, and 52 wk of age of Cobb grandparent females and Cobb MX males conventionally fed (CON), precision-fed (PF), or conventionally fed during lay after being precision-fed during rearing (PFCON).

¹BW (kg) was used as a covariate in the analysis. Thus, the slope coefficient represents the change in each carcass part with respect to a 1 kg BW increase (δ part/ δ BW).

^{a-c}Means within column within effect with no common superscript differ significantly (P < 0.05).

that a shift in body composition in PF birds, likely due to increased feeding frequency, may be a key factor affecting the onset of lay. It further suggests that feed restriction of commercial broiler breeders may be approaching a biological limit. In the current study, only 44% of PF treatment hens were in lay at the end of the production period, compared with 67% and 72% in the CON and PFCON treatments, respectively. Precisionfed hens that were laying must have been laying at a higher rate than CON and PFCON hens because their overall rate of egg production was similar at 52 wk. Birds that were not in lay at 52 wk of age had less than 50% of the abdominal fat and over 7% more breast muscle compared with hens that had at least 1 LYF at 52 wk. It is possible that some of the PF hens never laid any eggs because of an insufficient metabolic status to stimulate onset of laying.

Pre-pubertal Abdominal Fat Minimum BW, lean body mass, and carcass fat thresholds may be needed to commence and sustain egg production (Soller et al., 1984; Eitan et al., 2014). Thus, the relationship between abdominal fatpad and total carcass fat was explored. Shigeno (1973) reported a linear relationship between abdominal fatpad and total carcass fat in layers, y = 4.917+3.176x, where y was total carcass fat and x was abdominal fatpad, both as percentage of BW. Using data for broiler breeders (Zuidhof, unpublished data), an analogous equation was derived, y = 4.4922+4.1181x (Equation 1). Equation 1 robustly predicted the 68-wk broiler breeder total carcass fat (19.5%) from abdominal fatpad (4.6%) reported by Robbins et al. (1986), but overestimated 62-wk total carcass fat values reported by Yu et al. (1992b) in 3 of 4 treatments (average overprediction of 12%).

The extremely low fatpad weights in the current study prompted questions about minimum total carcass fat that may be required to initiate and sustain reproductive function. The carcass fat percentage of CON treatment and PF treatment pullets calculated using Equation 1 was 5.4% at 16 wk of age, and 6.9% and 7.6%, respectively, at 22 wk of age. Predicted carcass fat at 52 wk of age was 9.1% for hens, and 5.0% for roosters. Notably, the predicted total fat content of roosters did not increase from 16 to 52 wk of age. Although proportional abdominal fat in hens in lay at 52 wk was 2.19 times that of hens not in lay, Equation 1 predicted a 1.4-fold higher carcass fat for hens in lay compared with hens that had no LYF. Because the gap between broiler growth potential and recommended broiler breeder target BW is increasing (Renema et al., 2007b), it would follow that broiler breeding stock is becoming leaner. If fatness or metabolic thresholds required for the onset of laying are not met by a growing number of individuals in modern flocks, they would be expected to have reduced reproductive performance. To understand whether broiler genetic change over the last several decades has reduced carcass fat levels in breeders to a degree that may encroach on such thresholds, a history of broiler breeder carcass fatness around the time of photostimulation was investigated. The analysis focused on diets similar to commercial broiler breeder diets.

Eitan et al. (2014) reported a 30 to 50% reduction of carcass fat in meat type breeders over the 20 yr between 1980 and 2000, van Emous et al. (2015) reported 22-wk proportional abdominal fatpad weights of 0.68% when feeding Ross 308 broiler breeders a diet containing 14% CP in the grower and 15% CP in the pre-breeder phase. Using Equation 1, a total 22-wk carcass fat level of 7.3% was predicted. Over decades, however, selection for broiler growth, yield, and efficiency may be causing an unintended decrease in 22-wk carcass fat. Close to a decade prior, de Beer and Coon (2009) reported 22-wk total carcass fat at 9.6% and 9.4% for every day and skip-a-day fed Cobb 500 pullets, respectively, using 15.3% CP grower and 16.5%CP pre-breeder diets. Eight years prior, Miles et al. (1997) reported 22-wk total carcass lipid level at 11.6%in Cobb broiler breeder pullets fed a 14% CP diet. Seven vears prior to that, Bennett and Leeson (1990) reported a 22-wk total carcass fat level of 13.9% using a standard broiler breeder pullet diet containing 14.9% CP. Looking back through the literature over time, it is clear that carcass fat in pre-pubertal meat-type pullets has been decreasing. The effect of decreasing carcass fat in meat-type pullets on ovularche (first ovulation) and lifetime reproductive productivity has yet to be determined, but a 50% decrease in carcass fat levels observed in the current experiment compared with 30 years ago raises concerns that leanness may be approaching a biological limit for reproductive success in meat-type chickens.

Precision-fed broiler breeders had a 3.8% increase in fertility and a 1.3% reduction in egg weight CV compared with conventionally fed broiler breeders. Precision feeding increased broiler breeder flock uniformity dramatically over conventional feeding. However, the expected increase in reproductive efficiency as a result of the highly uniform flock was not achieved. Precision feeding increased feeding frequency, which in turn reduced diurnal variation in energy balance. This is the most likely cause of higher lean tissue growth and lower carcass fat: breast muscle ratios in PF birds. It is hypothesized that some of the PF pullets had either insufficient carcass fat reserves or an insufficient daily nutrient pulse to trigger the onset of sexual maturation. It is also likely that individual birds have different optimal BW at the onset of lay, and the current target BW was not sufficient for some birds, particularly when precision fed according to BW. Because reproductive success was observed in other trials where BW and ME intake restrictions were relaxed, it is hypothesized that breeder-recommended levels of feed restriction must be relaxed to accommodate changes in metabolism that result from increased feeding frequency in precision-fed broiler breeders.

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