Broiler growth and efficiency in response to relaxed maternal feed restriction

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ABSTRACT Broiler growth performance can be influenced by maternal BW, maternal age, and sex. The present study evaluated broiler growth and efficiency in response to increased maternal BW (relaxed level of maternal feed restriction). It was hypothesized that BW and fatness would increase, and efficiency would be reduced as maternal BW increased. Ten BW trajectories were applied to precision-fed Ross 708 female broiler breeders (n = 30) from 2 to 42 wk of age. Trajectories varied in prepubertal and pubertal growth phases from 2.5 to 22.5% above the recommended BW target. Additional unrestricted breeders (n = 6) were not limited to a maximum BW (fed ad libitum). Two 35 d experiments were conducted with precision-fed broilers from these breeders at 35 and 42 wk of age. Two analyses (full and restricted analysis scopes) were performed to evaluate broiler BW, feed conversion ratio (**FCR**) and carcass traits with maternal BW at photostimulation (22 wk of age) as a continuous effect, and maternal age and sex as discrete effects. The full scope included broilers from all hens (feed restricted and unrestricted). The restricted scope excluded broilers from unrestricted hens. Differences were reported at $P \leq 0.05$. For every kilogram increase in maternal BW, cumulative FCR increased by 0.235 and 0.471 g:g for broilers from all and feed restricted hens, respectively. Proportional gut weight of broilers from feed restricted hens decreased by 0.8244% per kilogram increase in maternal BW. Males were heavier than females on day 28 and 35, and broilers from 42-wk-old breeders were heavier than broilers from 35-wk-old breeders on day 0 and 35. Males from all hens were more feed efficient (1.318 g:g) than females (1.335 g:g) from day 29 to 35. Females from all and feed restricted hens had a greater proportional fat pad and breast muscle weight than males, and proportional breast muscle yield of broilers from 42-wk-old breeders was on average 1.04 times greater than that of broilers from 35-wk-old breeders. Maternal BW did not affect offspring BW, reduced cumulative FCR, and reduced gut weight in the restricted analysis scope.

Key words: precision livestock farming, intergenerational, maternal body weight, maternal age, offspring performance

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INTRODUCTION

Over the past few decades, genetic change in the broiler industry has heavily focused on fast and lean growth accompanied by high muscle yield (as reviewed by Tallentire et al., 2016). For example, growth rates of broiler strains used in 2005 increased by 400% compared with broiler strains used in 1957 (Zuidhof et al., 2014). A challenge the industry has faced is that breeder BW targets have remained relatively constant as growth potential of modern breeder and broiler lines continues to advance (Renema et al., 2007).

Broiler breeders are feed restricted during rearing, and to a lesser extent during lay, to achieve strict BW targets to optimize reproductive performance (Yu et al., 1992; Bruggeman et al., 1999). Restricted feed intake has been used to control follicular development and to improve reproductive performance in broiler breeders (Katanbaf et al., 1989; Hocking, 1993), which has increased the number of settable eggs for broiler chick production (Yu et al., 1992). However, new research suggests modern broiler breeders have unique optimal growth trajectories, some of which are above the current recommended BW targets, which is clearly emphasized in studies that have used precision feeding (**PF**) systems (Zuidhof, 2018; Hadinia et al., 2019). It was hypothesized that in combination with recent genetic change,

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some precision-fed broiler breeders with an optimum BW above the current recommended standard did not receive a sufficient amount of nutrients to reach an appropriate body composition to support high rates of egg production. Thus, there may be a need to increase BW targets to increase nutrient intake for precision-fed broiler breeders. This would not only influence management practices in the hatching egg industry, but address negative welfare issues related to feed restriction such as stress and hunger (D'Eath et al., 2009).

Maternal nutrition can influence offspring growth. Specifically in the context of meat-type chickens, various levels of dietary protein and energy increase egg and chick weights (Enting et al., 2007). In addition, increased maternal dietary protein and energy increased offspring BW and fatness, respectively (Moraes et al., 2014). Multiple studies have focused on intergenerational effects of maternal BW on broiler performance. Broilers from high BW hens (2,400 g at 20 wk of age) gained 2.4% more from 28 to 34 d of age than did broilers from standard BW hens (2,200 g at 20 wk of age; van Emous et al., 2015). Humphreys (2020) reported that broilers from high BW hens (21% above the recommended BW) were 3.9 and 4.1% heavier than broilers from standard BW hens on day 35 and 42, respectively. This research also found that gut and abdominal fat pad weights were 6.4 and 16.0% greater in broilers from high BW hens compared with standard BW hens, respectively. Recently, Bowling et al. (2018) assessed stress of feed restricted broiler breeders by measuring yolk corticosterone concentration. The authors found lower maternal BW (greater degree of maternal feed restriction) increased the concentration of yolk corticosterone, which might have reduced growth of male broilers at 42 d of age. Thus, more research is needed to determine the relationship between the degree of maternal BW and broiler growth performance.

In addition to maternal BW, offspring growth is affected by maternal age and sex. Broiler hatch BW increased with maternal age (Peebles et al., 1999; Tona et al., 2004; Iqbal et al., 2016). Male offspring have a greater final BW than females (van der Klein et al., 2017; Humphreys, 2020). Moreover, females are documented to have a greater proportion of breast muscle (Scheuermann et al., 2003; Zuidhof et al., 2014; van der Klein et al., 2017; Moraes et al., 2019) and fat pad (Lippens et al., 2010; Zuidhof et al., 2014; van der Klein et al., 2017; Moraes et al., 2019; Humphreys, 2020) than males.

Maternal BW has had no effect on broiler feed efficiency (van Emous et al., 2015; Humphreys, 2020). However, broiler efficiency may be influenced by BW. Chickens with a greater BW have greater maintenance requirements (Yu and Robinson, 1992; Latshaw and Moritz, 2009); therefore, efficiency may decrease with BW as birds allocate more nutrients to support growth and development.

The main objective of this study was to evaluate offspring growth performance in response to relaxed maternal feed restriction, implemented through various maternal BW trajectories. It was hypothesized that increased maternal BW (lesser degree of maternal feed restriction) would increase broiler BW, breast muscle yield and fatness, and reduce feed efficiency. A second objective was to investigate the effects of maternal age and broiler sex on offspring growth performance. It was additionally hypothesized that BW, breast muscle, liver, gut weights, and fatness would increase, and feed efficiency would decrease as maternal age increased. Furthermore, males would achieve a heavier BW, greater proportional breast weight, lower proportional fat pad weight, and would be more efficient than females.

MATERIALS AND METHODS

The animal protocol for the study 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).

Experimental Design

This offspring broiler study was designed as a completely randomized and controlled experiment, and included 2 replicated experiments that differed in maternal age: 35 and 42 wk of age (cohort 1 and 2, respectively). The experimental treatments were applied to the maternal broiler breeders. The maternal treatments consisted of 10 unique BW trajectories that were created from a multiphasic Gompertz growth model. The model estimated growth in prepubertal, pubertal, and postpubertal phases. Experimental trajectories varied in prepubertal and pubertal growth phases starting from the Ross 708 recommended BW target (CON; Aviagen, 2016a) up to 22.5% above the Ross 708 recommended BW target, in 2.5% increments (CON+2.5%, CON+5%, … CON+22.5%). Three female broiler breeders were assigned to each trajectory and were feed restricted to reach their respective target BW. Six additional broiler breeders were assigned to an unrestricted group, meaning they were fed every time they went to the feeding station and were not limited to a maximum BW. In the offspring study, which is the focus of the current article, each broiler was considered an experimental unit.

Source Flock

Stocks and Management The source flock consisted of Ross 708 broiler breeder females (n = 36) housed with Aviagen Yield Plus males (n = 8) in a single environmental chamber with 2 PF stations at a stocking rate of 3.2 birds/m^2. Birds were fed a commercial standard starter crumble diet from 0 to 5 wk (2,726 kcal ME, 21% CP, and 1.0% Ca), a commercial broiler breeder grower mash from 6 to 26 wk (2,799 kcal ME, 15% CP, and 0.8% Ca) and a broiler breeder layer mash from 26 wk to the end of the experiment (2,798 kcal ME, 15% CP, and 3.4% Ca). Females were fed to achieve

BW targets specific to their trajectory and males were precision-fed in accordance with the Yield Plus male standard BW profile (Aviagen, 2016b). The photoschedule was 24L:0D at 100 lx from day 0 to 3, then reduced to 8L:16D at 15 lx on day 4. Light intensity was reduced to 5 lx on day 26 and remained constant until wk 21 to minimize feather pecking. The females were photostimulated at 22 wk of age by increasing the photoperiod to 11L:13D (20 lx). Day length was further increased to 12L:12D (35 lx) at 23 wk, and 13L:11D (50 lx) at wk 24. Each PF station had green LED lights located above the entry doors and feeders of the feeing stations (2 lx) as minimal illumination to allow birds to navigate through the feeding station during the scotophase. The temperature was set at 34.5°C on day 0 and decreased by 0.5°C daily until day 22 after which the set temperature remained constant at 23.5°C. A neck tag was applied on day 0 for individual identification. A wing tag equipped with a radiofrequency identification (**RFID**) transponder was applied to the right wing web of each bird on day 7 to allow the PF stations to identify each individual. All birds were fed individual meals using the PF system (Zuidhof et al., 2019). If the bird's BW was greater than or equal to the programmed BW target, it was gently ejected from the station without gaining access to feed. If the bird's BW was below the BW target, it was given access to a 65 g of feed for a duration of 90 s.

Egg Collection Eggs were collected from the source flock over a 7 d period at 35 and 42 wk of age and stored at 18°C before incubation. The hen ID, date, and egg weight were recorded on each egg. At the end of each day, eggs were examined and selected for incubation based on egg shape, shell quality, egg weight, and cleanliness. Unsettable eggs, defined to include those that were misshapen, thin shelled, weighed less than 52 g or covered with more than 3 mm of dirt, feces or blood were discarded.

Stocks and Management

Cohort 1 At 35 wk of age, 167 eggs were collected over 7 d from the broiler breeder source flock, then set in an incubator (30% RH, 37.5°C). Eggs were candled on d 7 of incubation and discarded if infertile (n = 12). On d 18 of incubation, eggs were weighed, transferred into pedigree hatching baskets, and placed in a hatcher (30% RH, 37.5°C). At hatch, chicks (n = 105) were feather-sexed and randomly assigned to 1 of 4 environmental chambers that contained 3 PF stations and ad libitum access to water (n = 1 chamber of 27 chicks; n = 3 chambers of 26 chicks). A wing tag equipped with an RFID transponder was applied to the right wing web of each chick on d 7 for individual identification within the PF stations.

Cohort 2 At 42 wk of age, 158 eggs were collected over 7 d from the broiler breeder source flock, then placed in an incubator (30% RH and 37.5°C). Eggs were candled on d 7 of incubation and discarded if infertile (n = 12). On d 18, eggs were weighed, transferred into pedigree hatching baskets and placed in a hatcher (30% RH and 37.5°C). At hatch, chicks (n = 112) were feather-sexed and randomly assigned to 1 of 4 environmental chambers with 3 PF stations and ad libitum access to water (n = 26, 29, 23, and 34 chicks per chamber). A wing tag equipped with an RFID transponder was applied to the right wing web of each chick on d 7 for individual identification within the PF stations.

Diets, Lighting and Temperature Birds were fed commercial broiler diets: a starter crumble from d 0 to 10 (3,044 kcal ME, 23.0% CP, and 1.0% Ca), a grower crumble from 11 to 24 d (3,091 kcal ME, 20.5% CP, and 0.9% Ca) and a finisher pellet from d 25 to 35 (3,170 kcal ME, 21.0% CP, and 0.8% Ca). The photoschedule was 23L:1D (16 lx) from d 0 to 3, and decreased by 1 h of light each day until d 7 where the photoperiod remained at 19L:5D (8 lx) for the duration of the experiment. Temperature was set at 34°C on d 0 and decreased by 0.5°C per day until d 28 after which it remained constant at 20.0°C.

Precision Feeding System

The PF system design and function has been described elsewhere (Zuidhof et al., 2019). Briefly, the PF system provided multiple meals to individual broilers throughout the day, based on live BW. Each broiler voluntarily entered the station where it was recognized by its unique RFID. Broilers were fed ad libitum meaning they were given access to feed on every station visit. The duration of each feeding bout was 60 s. During each feeding bout, broilers had access to 75 g of feed from 0 to 13 d, which was reduced to 65 g from d 14 to 35 to minimize feed wastage. Body weight and feed intake for every feeding bout was recorded in a database along with the RFID.

Data Collection

Body Weight and Average Daily Feed Intake Body weight was manually recorded for each bird daily from d 0 to 11. Body weight was recorded in the PF database on each station visit beginning on d 12 for the remainder of the experiment (on average, each bird visited the station 417 and 407 times for cohort 1 and 2, respectively). Body weight on d 35 was recorded using a hanging scale. To calculate feed conversion ratio (**FCR**), ADFI was recorded in the PF database from d 8 (cohort 1) and 9 (cohort 2) during individual feeding because it was not possible to accurately measure ADFI for each bird before individual feeding. During the experiment for cohort 2, there was an unexpected PF system software update on d 7 and 8 which delayed individual feeding mode by 1 d.

Carcass Traits The broilers were euthanized by cervical dislocation and immediately dissected on d 35. Breast muscle (pectoralis major and minor muscles), liver, heart, abdominal fat pad, and the gastrointestinal tract (gut; 1 cm above the crop to the end of the colon) weights were recorded. The gastrointestinal tract was not completely emptied; however, all PF stations were closed 12 h before euthanasia to ensure the amount of contents in the gastrointestinal tract was low, and consistent among broilers. Sex was confirmed at the time of dissection.

Statistical Analysis

All statistical analyses were performed using the MIXED procedure in SAS (Version 9.4. SAS institute, Inc., Cary, NC). Egg weight was evaluated as a one-way ANOVA with maternal age the categorical effect, and maternal BW at photostimulation as a covariate. Maternal BW at photostimulation was used as a proxy for differences in BW across BW trajectories. The day on which eggs were collected was used as the random effect with individual breeder hen as the subject. Body weight, FCR, and carcass traits were evaluated under 2 separate analyses with distinct scopes. The first analysis included broilers from all broiler breeders (full scope; including feed restricted and unrestricted broiler breeders), and the second analysis included broilers from feed restricted broiler breeders only (restricted scope; excluded the unrestricted broiler breeders). An ANOVA was conducted with maternal BW at photostimulation as the main effect (regressor), and maternal age and sex as categorical effects on broiler BW, FCR, and carcass traits. Similar to the EW analysis, maternal BW at photostimulation was used as a proxy for differences in BW across BW trajectories. Owing to convergence issues arising from model complexity, the intercept for each hen (maternal subject) was used as a random effect, rather than pen and individual broiler. Treatment effects on BW were evaluated on d 0, 7, 14, 21, 28, and 35. Feed conversion ratio was analyzed in 4 periods (d 7 to 14, 15 to 21, 22 to 28, and 29 to 35) and from d 7 to 35 (cumulative FCR). Least squares means were adjusting using Tukey's range test and were compared using the DIFF option. Differences were reported when $P \leq 0.05$. Trends were reported when $0.05 < P \leq 0.10$.

RESULTS AND DISCUSSION

Results are presented separately for each of the 2 analysis scopes. The full scope included broilers from feed restricted and unrestricted breeders. The restricted scope included broilers from feed restricted breeders only, excluding offspring from the unrestricted breeders. Interactions of maternal age, maternal BW, and sex were not significant and were therefore removed from the statistical model.

Interpretation of Regression Coefficients

Regression coefficients for maternal BW were reported for offspring BW (Table 1), FCR (Table 2), and carcass traits (Table 3). The regression coefficient explained the effect of each dependent variable (BW, FCR, and carcass traits) per kilogram increase in maternal BW. A negative sign of the regression coefficient indicated that the value of the dependent variable decreased with increasing maternal BW. A positive sign of the regression coefficient indicated that the value of the dependent variable increased with increasing maternal BW.

Body Weight

Full Scope There was no effect of maternal BW on broiler offspring BW from 0 to 35 d of age (Table 1). On d 0, BW of offspring from 42-wk-old breeders was 1.06 times that of offspring from 35-wk-old breeders. On d 35, broilers from 42-wk-old breeders were 95 g heavier than those from 35-wk-old breeders. By contrast, on d 7, offspring from 42-wk-old breeders weighed 23 g less than those from the 35-wk-old flock. Offspring from the 42-wk-old flock tended to be heavier than those from the 35-wk-old flock on d 21 ($P = 0.088$, Table 1). Males were 95 and 126 g heavier than females on d 28 and 35, respectively (Table 1).

Restricted Scope Offspring BW was not affected by maternal BW (Table 1). On d 0 and 35, BW of offspring from 42 wk old breeders were heavier (44.9 and 2,131 g) than that of offspring from 35-wk-old breeders (42.5 and 2,036 g), respectively. On d 7 however, BW of offspring from 35-wk-old breeders was 1.15 times that of offspring from 42-wk-old breeders. On d 21, offspring from 42-wk-old breeders tended to be 1.05 times heavier than those from 35-wk-old breeders. On d 28 and 35, males were 95 and 162 g heavier than females, respectively (Table 1).

Body weight, independent of the analysis scope, was not affected by maternal BW, which does not support the original hypothesis that BW would increase as maternal BW increased. Thus, broiler breeders reared to achieve BW targets from 2.5 to 22.5% above the recommended targets or fed ab libitum produced offspring that had similar BW over a 35 d grow cycle. This is inconsistent with Humphreys (2020) who reported that offspring from hens reared 21% above the recommended BW target (high BW) were 3.9% heavier than offspring from hens reared on a standard BW on d 35. Moreover, van Emous et al. (2015) observed that broilers from high BW hens (9% above standard BW curve) weighed 1.4% more than those from standard BW hens on d 35. In contrast with the present study, Humphreys (2020) and van Emous et al. (2015) found that broiler hatch weight did not differ between high and standard BW hens. Egg and chick weights are positively correlated (Wilson, 1991; Tona et al., 2004; Lourens et al., 2006; Iqbal et al., 2016). Moreover, EW increased with hen BW (McDaniel et al., 1981). Reproductive performance of the broiler breeders in the present study was reported by Zukiwsky et al. (2020). Consistent with previous literature, the authors found that EW increased with BW. In the present study, eggs from the 42-wk-old breeders on average weighed 65.0 g, which was 3.3 g heavier than those from the 35-wk-old breeders ($P < 0.001$). Thus,

Table 1. Body weight of broiler offspring on d 0, 7, 14, 21, 28, and 35 as per the full[1] and restricted[2] scope analyses.

Scope	Effect	MA	Sex	Age (d)											
				0	SEM	7	SEM	14	SEM	21	SEM	28	SEM	35	SEM
Full	Continuous			g/kg											
	BW at PS			0.484	0.667	−1.811	2.309	−8.692	7.255	−17.339	17.075	−32.281	27.712	−36.987	35.042
	Categorical			g											
	MA (wk)	35		42.5^{b}	0.4	164^{a}	2.0	424	6.5	860	13.8	1,479	24.0	2,022^{b}	30.4
		42		45.1^{a}	0.4	141^{b}	2.0	424	5.9	895	14.6	1,531	24.6	2,117^{a}	32.4
	Sex		M	43.9	0.4	152	2.0	430	6.4	895	16.3	1,552^{a}	28.6	2,151^{a}	36.6
			F	43.6	0.4	152	2.0	419	5.9	860	11.9	1,457^{b}	19.2	1,989^{b}	25.2
	Source of variation			Probability											
	BW at PS			0.47		0.44		0.24		0.32		0.25		0.30	
	MA			<0.001		<0.001		0.99		0.088		0.13		0.033	
	Sex			0.60		0.92		0.21		0.083		0.006		<0.001	
Restricted	Continuous			g/kg											
	BW at PS			0.327	2.830	11.088	7.734	34.186	26.054	76.415	63.726	95.928	100.640	96.099	125.100
	Categorical			g											
	MA (wk)	35		42.5^{b}	0.4	164^{a}	2.1	426	7.2	865	15.16	1,489	26.0	2,036^{b}	32.0
		42		44.9^{a}	0.5	142^{b}	2.1	430	5.9	905	15.50	1,545	25.5	2,131^{a}	34.6
	Sex		M	43.9	0.5	152	2.1	432	6.8	900	17.4	1,561^{a}	30.0	2,160^{a}	39.0
			F	43.5	0.4	154	2.1	424	6.4	870	12.9	1,472^{b}	20.6	2,007^{b}	26.5
	Source of variation			Probability											
	BW at PS			0.91		0.16		0.20		0.24		0.35		0.45	
	MA			<0.001		<0.001		0.62		0.066		0.13		0.047	
	Sex			0.52		0.61		0.37		0.16		0.016		0.002	

[a,b] LSMeans within analysis scope, column, and effect with no common superscript differ ($P < 0.05$).

The regression coefficient was reported for maternal BW at photostimulation (PS) as a continuous effect, and LSMeans were reported for categorical effects maternal age (MA) and sex.

[1] Full scope analysis included broiler offspring from feed restricted and unrestricted hens. Feed restricted hens were reared according to 10 unique BW trajectories as maternal treatments that varied in prepubertal and pubertal phases of growth up to 22.5% above the recommended Ross 708 BW target, in 2.5% increments. Six additional hens were unrestricted (not limited to a maximum BW).

[2] Restricted scope analysis excluded broiler offspring from unrestricted broiler breeders.

Table 2. Cumulative FCR and FCR over 4 periods from 7 to 35 d of age of broiler offspring as per the full[1] and restricted[2] scope analyses.

				Age (d)									
				7 to 14		15 to 21		22 to 28		29 to 35		Cumulative FCR	
Scope	Effect	MA	Sex	FCR	SEM	FCR	SEM	FCR	SEM	FCR	SEM	FCR	SEM
Full	Continuous			g:g/kg									
	BW at PS			0.003	0.013	0.006	0.009	0.005	0.007	0.004	0.007	0.235	0.065
	Categorical			g:g									
	MA (wk)	35		0.901	0.014	1.059	0.008	1.225	0.006	1.319	0.006	1.489	0.066
		42		0.929	0.013	1.068	0.008	1.231	0.006	1.334	0.005	1.529	0.064
	Sex		M	0.912	0.014	1.060	0.008	1.223	0.006	1.318^{b}	0.006	1.484	0.066
			F	0.919	0.013	1.067	0.009	1.233	0.006	1.335^{a}	0.005	1.534	0.064
	Source of variation			Probability									
	BW at PS			0.81		0.55		0.46		0.52		<0.001	
	MA			0.14		0.43		0.48		0.071		0.67	
	Sex			0.71		0.57		0.23		0.040		0.59	
Restricted	Continuous			g:g/kg									
	BW at PS			−0.091	0.051	−0.081	0.034	−0.046	0.027	−0.003	0.028	0.471	0.181
	Categorical			g:g									
	MA (wk)	35		0.900	0.016	1.053	0.009	1.221	0.006	1.317	0.008	1.420	0.063
		42		0.926	0.014	1.066	0.009	1.229	0.006	1.334	0.005	1.457	0.058
	Sex		M	0.913	0.016	1.059	0.009	1.222	0.006	1.319	0.007	1.443	0.056
			F	0.913	0.015	1.060	0.009	1.228	0.006	1.332	0.006	1.434	0.056
	Source of variation			Probability									
	BW at PS			0.076		0.026		0.10		0.93		0.010	
	MA			0.23		0.31		0.36		0.071		0.67	
	Sex			0.99		0.95		0.49		0.14		0.92	

[a,b]LSMeans within analysis scope, column, and effect with no common superscript differ ($P < 0.05$).

The regression coefficient was reported for maternal BW at photostimulation (PS) as a continuous effect, and LSMeans were reported for categorical effects maternal age (MA) and sex.

[1] Full scope analysis included broiler offspring from feed restricted and unrestricted hens. Feed restricted hens were reared according to 10 unique BW trajectories as maternal treatments that varied in prepubertal and pubertal phases of growth up to 22.5% above the recommended Ross 708 BW target, in 2.5% increments. Six additional hens were unrestricted (not limited to a maximum BW).

[2] Restricted scope analysis excluded broiler offspring from unrestricted broiler breeders.

greater hatch BW of offspring from 42-wk-old breeders might have been due to greater EW.

Similar effects of maternal age and sex were observed between both analysis scopes, which was consistent with the hypotheses that BW would increase with maternal age, and males would be heavier than females. Specifically on d 0 and on 35, offspring from the 42-wk-old breeders were heavier than those from 35-wk-old breeders. This was expected as hatch weight (Peebles et al., 1999; Tona et al., 2004; Ulmer-Franco et al., 2010; El Sabry et al., 2013; Iqbal et al., 2016) and final BW (Ulmer-Franco et al., 2010; El Sabry et al., 2013) are reported to increase with maternal age. Furthermore, male offspring from both analysis scopes were heavier than females on d 28 and 35. Bowling et al. (2018) evaluated growth performance of broilers from feed restricted hens with low (3.4), medium (3.5), or high (3.9 kg) BW. The authors found no difference in offspring BW from 0 to 35 d of age; however, male offspring from high BW hens were 227.4 g heavier than those from high BW hens on d 42. The authors reported that yolks from low BW hens had a corticosterone concentration 1.21 times greater than that of medium BW hens, and hypothesized that maternal feed restriction-induced stress might have reduced male offspring BW on d 42. It is possible that in the present study, sex-dependent differences in BW at the end of the growing cycle might have been due to the reduced stress as a result of increased maternal BW and concomitant relaxed levels of feed restriction.

Feed Efficiency

Full Scope Feed efficiency was not affected by maternal BW during the 7 to 14, 15 to 21, 22 to 28, and 29 to 35 d of age periods (Table 2). However, cumulative FCR over the whole study (7 to 35 d) increased by 0.235 g:g/kg of maternal BW (R2 = 0.208, $P < 0.001$). From d 29 to 35, FCR tended to be lower of offspring from 35-wk-old breeders (1.319) than those from 42-wk-old breeders (1.334 g:g; $P = 0.071$). Males had a significantly lower FCR (1.318) than females (1.335 g:g) from 29 to 35 d of age.

Restricted Scope For every kilogram increase of maternal BW, offspring FCR decreased by 0.081 g:g from 15 to 21 d of age (R2 = 0.171, $P = 0.026$). In addition, cumulative FCR increased by 0.471 g:g/kg of maternal BW (R2 = 0.048, $P = 0.010$). Offspring FCR tended to decrease by 0.091 and 0.046 g:g per kilogram increase in maternal BW from d 7 to 14 ($P = 0.076$) and 22 to 28 ($P = 0.10$), respectively. There were no significant effects of maternal age and sex on FCR (Table 2); however, from d 29 to 35, offspring from 35-wk-old breeders tended to be 1.3% more efficient than those from 42-wk-old breeders ($P = 0.071$).

Table 3. Breast, liver, heart, abdominal fat pad, and gut weight as a percentage of live BW of 35 d old broiler offspring as per the full[1] and restricted[2] scope analyses.

Scope	Effect	MA	Sex	Breast	SEM	Liver	SEM	Heart	SEM	Fat pad	SEM	Gut	SEM
Full	Continuous			% yield/kg									
	BW at PS			−0.409	0.222	0.021	0.024	−0.002	0.010	−0.001	0.037	0.097	0.116
	Categorical			% of live BW									
	MA (wk)	35		20.93^{b}	0.20	1.80^{b}	0.02	0.56	0.01	1.33	0.03	6.20	0.10
		42		21.70^{a}	0.22	1.85^{a}	0.02	0.58	0.01	1.40	0.03	6.06	0.10
	Sex		M	20.83^{b}	0.23	1.83	0.02	0.60^{a}	0.01	1.23^{b}	0.03	6.26	0.09
			F	21.81^{a}	0.18	1.82	0.02	0.55^{b}	0.01	1.45^{a}	0.03	5.99	0.12
	Source of variation			Probability									
	BW at PS			0.073		0.38		0.83		0.98		0.41	
	MA			0.009		0.047		0.17		0.15		0.33	
	Sex			0.001		0.54		<0.001		<0.001		0.06	
Restricted	Continuous			% yield/kg									
	BW at PS			0.919	0.851	−0.117	0.084	−0.052	0.040	−0.007	0.153	−0.824	0.339
	Categorical			% of live BW									
	MA (wk)	35		21.11^{b}	0.22	1.80	0.02	0.56	0.01	1.35	0.03	6.15	0.10
		42		21.78^{a}	0.24	1.85	0.02	0.58	0.01	1.38	0.04	6.01	0.11
	Sex		M	21.00^{b}	0.20	1.83	0.02	0.59^{a}	0.01	1.27^{b}	0.04	6.24^{a}	0.13
			F	21.90^{a}	0.25	1.81	0.02	0.55^{b}	0.01	1.45^{a}	0.03	5.93^{b}	0.08
	Source of variation			Probability									
	BW at PS			0.29		0.18		0.20		0.96		0.022	
	MA			0.038		0.13		0.27		0.57		0.35	
	Sex			0.005		0.46		0.004		<0.001		0.039	

^{a,b}LSMeans within analysis scope, column, and effect with no common superscript differ ($P < 0.05$).

The regression coefficient was reported for maternal BW at photostimulation (PS) as a continuous effect, and LSMeans were reported for categorical effects maternal age (MA) and sex.

[1] Full scope analysis included broiler offspring from feed restricted and unrestricted hens. Feed restricted hens were reared according to 10 unique BW trajectories as maternal treatments that varied in prepubertal and pubertal phases of growth up to 22.5% above the recommended Ross 708 BW target, in 2.5% increments. Six additional hens were unrestricted (not limited to a maximum BW).

[2] Restricted scope analysis excluded broiler offspring from unrestricted broiler breeders.

Cumulative FCR of offspring from both analysis scopes increased as maternal BW increased. This suggests that offspring from heavier BW hens were less efficient than those from heavy BW hens over a 7 to 35 d growth period, which is consistent with they hypothesis. Cumulative FCR might have been influenced by individual broiler variation in ADFI and motivation to seek feed within the PF system might have also influenced FCR. Feed conversion ratio of offspring from the restricted scope analysis decreased from 15 to 21 d of age as maternal BW increased. In other words from d 15 to 21, in the range of restricted maternal BW trajectories that were studied, offspring from heavy BW hens were less efficient then those from lighter BW hens.

Carcass Traits

Full Scope There were no significant effects of maternal BW on the proportions of breast muscle, liver, heart, fat pad, and gut weights (Table 3). The proportion of breast muscle weight tended to decrease by 0.41%/kg of maternal BW ($R^2 = 0.190$, $P = 0.073$). Proportional breast weight of offspring from 42-wk-old breeders was 1.04 times that of offspring from 35-wk-old breeders. Similarly, proportional liver weight of offspring from 42-wk-old breeders was 1.06 times greater than that of offspring from 35-wk-old breeders. Proportional breast muscle weight of females was 1.05 times that of males, and the proportional weight of fat pad for females was 1.15 times greater than that of males (Table 3). Proportional heart weight was 1.20 times greater in males than in females. Proportional gut weight of males tended to be 1.05 times greater than that of males ($P = 0.06$).

Restricted Scope Proportional gut weight decreased by 0.82%/kg of maternal BW ($R^2 = 0.114$, $P = 0.022$), whereas proportional breast muscle, liver, heart, and fat pad weights were not affected by maternal BW (Table 3). The proportion of breast muscle yield was 1.03 times greater in offspring from 42-wk-old breeders than those from 35-wk-old breeders. Similar to the full scope analysis, various proportional organ weights were affected by sex (Table 3). Specifically, proportional breast and fat pad weights of females were 1.04 and 1.14 times that of males, respectively. Proportional heart and gut weights in males were 1.05 times greater than those in females, respectively.

There were minimal effects of maternal BW on carcass traits of offspring from both the full and restricted analysis scopes. Among offspring in the restricted analysis scope, gut weight decreased as maternal BW increased. A large gut is associated with increased nutrient absorption (Jackson and Diamond, 1996; further reviewed by Tallentire et al., 2016) and was also associated with increased ADG (Humphreys, 2020). In the restricted analysis scope of the present study, offspring from low BW hens had larger guts than those from high BW hens, which could have resulted in a lower FCR

(Table 2). Thus, a smaller gut weight as a result of increased maternal BW may reduce broiler efficiency. The proportion of fat pad weight was not influenced by maternal BW of offspring from the full and restricted analysis scopes (Table 3). This was interesting to note because other literature reported the proportion of fat in broilers increased as a result of increased maternal BW (van der Waaij et al., 2011; Humphreys, 2020).

In both analysis scopes, offspring from 42-wk-old breeders had greater proportional breast muscle yield than those from 35-wk-old breeders. This may be explained by the natural allometric growth of breast muscle in broilers. Previous literature has reported that breast muscle weight increased with BW (Scheuermann et al., 2003; Zuidhof et al., 2014; van der Klein et al., 2017), which is consistent with the current results as offspring from 42-wk-old breeders were heavier than those from 35-wk-old breeders on d 35. In addition, proportional liver weight increased with maternal age in offspring from the full analysis scope; however, this was not observed in offspring from the restricted analysis scope. The liver is an important metabolic organ that supports growth and development. A heavy BW broiler might have a larger liver to support greater maintenance requirements compared with a lighter BW broiler. Thus, greater proportional liver weight might be related to greater BW on d 35 of broilers from 42-wk-old breeders than those from 35-wk-old breeders in the full analysis scope.

A primary result of decades of genetic selection has increased breast muscle yield and decreased the proportion of carcass fat (Zuidhof et al., 2014). Females in both analysis scopes had greater proportional weight of breast muscle and abdominal fat pad than males. Moreover, proportional heart weight of males was greater than that of females. These results were expected because it is well established that females have a larger proportion of breast muscle (Grey et al., 1982; Young et al., 2001; Moraes et al., 2014, 2019; Zuidhof et al., 2014) and abdominal fat pad (Brake et al., 1993; Moraes et al., 2014; Zuidhof et al., 2014; Humphreys, 2020) than males, whereas males have a greater proportional heart weight than females (Brake et al., 1993; Zuidhof et al., 2014; Humphreys, 2020). In the restricted scope analysis, males had a greater proportional gut weight than females, which is consistent with van der Klein et al. (2017) and Humphreys (2020). The gut is responsible for nutrient absorption, which plays a key role in metabolism to support growth and muscle development. Specific to the restricted analysis scope, males were heavier than females on d 35. Thus, males might have had a greater proportional gut weight than females to support maintenance requirements associated with a greater BW.

In conclusion, there were several notable effects of maternal age and sex on BW, FCR, and carcass traits. Consistent with previous literature and the current hypotheses, BW increased with maternal age, and males were heavier than females. Moreover, females had a greater proportion of breast muscle yield and abdominal fat than males. In the range of restricted maternal BW trajectories that were studied, relaxed maternal feed restriction and unrestricted feed intake did not affect broiler offspring BW during the entire growth cycle. Consistent with the hypothesis, cumulative FCR from d 7 to 35 decreased as maternal BW increased among broilers from the full and restricted analysis scopes. This reduction in offspring feed efficiency may have been due to increased maintenance requirement as BW increased. In the range of maternal BW trajectories studied, the impact on offspring carcass traits was less than expected. Notably, proportional gut weight of broiler offspring in the restricted scope analysis decreased with increasing maternal BW, which might have contributed to reduced feed efficiency. Overall, it was concluded that increased maternal BW up to 22.5% above the recommended BW and unrestricted growth had little impact on broiler growth performance. This suggests that increasing female broiler breeder BW targets to lower the severity of feed restriction would reduce gut weight and increase feed efficiency in broiler offspring.

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DISCLOSURES

The authors declare no conflict of interest.

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