# Evolution of maternal feed restriction practices over 60 years of selection for broiler productivity

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**ABSTRACT** The effect of commercial selection by poultry breeders on the growth, efficiency, and sexual maturity of broiler breeders was studied using 2 University of Alberta Meat Control strains unselected since 1957 and 1978 (**AMC-1957** and **AMC-1978**, respectively) and 2 strains originating from the University of Arkansas; 1995 Random-bred (**1995RB**) and 2015 Random-bred (**2015RB**). A study with a 4 × 2 factorial arrangement was conducted with the 4 strains fed at either ad libitum, or restricted levels to achieve a current commercial breeder target BW profile. Growth rate, feed intake, feed efficiency, age at sexual maturity, carcass components, and body conformation were measured. To assess reproductive development, birds were assigned to 2 fates: dissected at photostimulation or dissected after the second oviposition. At 22.4 wk of age, the restricted-fed AMC-1957, AMC-1978, 1995RB, and 2015RB reached 100, 61, 46, and 38% of their ad libitum-fed counterparts' BW, respectively. During the rearing phase, the amount of feed needed to maintain restricted-fed birds on the target BW was 99.4, 57, 29.5, and 24.9% of their ad libitum-fed counterparts for AMC-1957, AMC-1978, 1995RB, and 2015RB, respectively. Feed restricted birds in the 2015RB had lower heat production relative to the AMC-1957 and AMC-1978, which shows that modern strains utilized feed more efficiently compared to the antique strains. This might be related to the increasing severity of feed restriction of broiler breeders over the past 60 years. Relative to AMC-1957 and AMC-1978 strains, the 1995RB and 2015RB strains had heavier breast muscle and lower fat pad weight. Although the pubertal threshold for age and BW have increased over the last 6 decades, changes in selection programs for feed efficiency have resulted in broiler breeders that prioritize nutrient allocation to growth and breast development rather than adipose storage. As a result, feed restricted modern broiler breeders may have marginally sufficient fat resources to support reproduction.

**Key words:** broiler breeder, sexual maturity, quantitative feed restriction, genetic progress, feed efficiency

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## INTRODUCTION

Genetic progress in broiler chicken breeding has been well documented in terms of changes in growth rate, carcass morphology, and feed efficiency (Emmerson, 1997; Hunton, 2006). After decades of quantitative genetic selection, modern broiler chickens have substantially greater growth rates, carcass yield and feed efficiency than birds from 1957 (Havenstein et al., 2003a,b; Zuidhof et al., 2014). A comprehensive study focusing on growth and carcass traits of broiler strains of University of Alberta Meat Control (**AMC**) 1957, 1978 and a 2005 commercial Ross 308 strain showed that from 1957 to 2005, growth rate to 56 d increased by over 400%, with a halving of the feed required to produce a 42-d broiler (Zuidhof et al., 2014). This was associated by changes in broiler body conformation. For instance, breast muscle yield increased by 79% in males and 85% in females as a result of the selection of broilers.

In broiler breeders, the parent stock of meat-type chickens, impaired reproductive efficiency has been associated with increasing broiler performance (Renema et al., 2007; Zuidhof et al., 2007). For the past 45 yr, feed restriction has been necessary for broiler breeders during the rearing and laying periods to permit normal laying cycles and to reduce obesity-related disorders (Richards et al., 2010). Erratic oviposition and defective egg syndrome (**EODES**, Jaap and Muir, 1968; van Middlekoop, 1972; van Middlekoop and Siegel, 1976) has been used to describe breeder hens who display laying outside of the normal pattern (Etches, 1990) and lay



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an increased incidence of double-yolk eggs and eggs with poor shell quality. Selection for reproductive output in broiler breeder females has indirectly influenced the development of ovarian follicles in such a way to increase the number of large yellow follicles (**LYF**; greater than 1 cm diameter). Excess LYF (more than 8 LYF) in the ovary of full-fed breeders are grouped in double or triple hierarchies, which increases the potential for follicular hierarchy and erratic laying. Further, modern strains are less susceptible to developing the ovarian follicular hierarchy structure as a result of overfeeding (Renema et al., 2007; Eitan and Soller, 2009; Decuypere et al., 2010).

Broiler breeder feed restriction is typically implemented through feeding sufficient quantities to achieve a target BW for age recommended by primary breeders. A paradox exists where substantial feed restriction is necessary to prevent metabolic, reproductive, and skeletal problems, but feed restriction also has negative impacts on production and animal welfare (Decuypere, et al., 2010). Over time, the genetic potential of broiler lines for growth, efficiency, and meat yield has increased dramatically (Zuidhof et al., 2014), while comparatively, the target BW for broiler breeders has remained static. More specifically, in 1979, the breeder target BW was 53% of the broiler at 6 weeks of age, which reduced to 27% in 2005 and 22.5% in 2021 (Renema et al., 2007; Aviagen, 2019, 2021). Thus, the gap between growth potential of broilers and broiler breeder target BW is increasing, which has resulted in increased feed restriction severity. Since the 1990s, research has shown that feed restriction levels cause hunger and this practice is a welfare issue (Hocking et al., 2002; Mench, 2002; van Krimpen and de Jong, 2014). Several studies have shown that feed-restricted broiler breeders show behaviors indicative of frustration (increase in activity level and decrease time spent for resting, eating, and comfort behavior); more foraging behavior; pacing; stereotypic object pecking; polydipsia; and hyperactivity (Hocking et al., 2001, 2002; de Jong et al., 2003; Puterflam et al., 2006; Nielsen et al., 2011; Riber et al., 2021).

Although broiler stocks and their parents have become leaner through genetic selection (Zuidhof et al., 2014; van Emous et al., 2015), increasing severity of feed restriction is likely a major contributor to reduced carcass fat levels in broiler breeders (Zuidhof, 2018). Havenstein et al. (2003b) fed a 2001 broiler strain (Ross 308) and a 1957 strain a diet typical of 2001 and found that the 2001 strain had a lower portion (% of BW) of abdominal fat and carcass fat at 43 d (1.4 and 13.7%, respectively) compared to the 1957 strain at 85 d of age (2.0 and 17.9%). Carcass fat content of severely feed-restricted modern broiler breeders may not be adequate to advance pubertal development and ultimately, ovulation. Allowing increased feeding frequency while maintaining target BW is believed to have caused metabolic changes leading to reduced fatness that prevented sexual maturation and reduced egg production performance in precision-fed breeder and grandparent flocks (Hadinia et al., 2018; van der Klein et al., 2018a; Zuidhof, 2018). Feeding frequency can affect metabolic responses and reproductive efficiency; variations in nutrient intake and subsequent energy status are communicated to the liver and hypothalamic-pituitary axis by alterations in the plasma levels of hormones (e.g., insulin, glucagon, T3) and metabolites such as glucose and free fatty acids (Sun et al., 2006; Moradi et al., 2013). For instance, de Beer et al. (2008) found that skip-a-day feeding was less efficient in feed utilization for growth and egg production than everyday feeding in breeders due to the need to deposit and remobilize nutrients during the fasting period. Shortening fasting length, through increasing feeding frequency, improved feed utilization efficiency that enhanced egg production rate and egg weight as well as reduced hepatic lipogenesis (Richards et al., 2003; Moradi et al., 2013).

This paper represents further research into the AMC-1957 and AMC-1978 lines of broilers reported earlier (Zuidhof et al., 2014) and also includes a 1995 Random-bred (**1995RB**) strain (Harford et al., 2014) and a 2015 Random-bred (**2015RB**) line (Orlowski et al., 2020) both made up of commercially available parent stock genetics at the time of development. The objectives of the current study were to re-evaluate the growth, efficiency, and yield characteristics of the aforementioned lines and also to investigate the timing of sexual maturation of female stocks under conditions of ad libitum feeding or nutrient restriction to a modern broiler breeder BW standard. Furthermore, the study evaluated how the degree of feed restriction has changed over the last seven decades to maintain birds on a modern-day broiler breeder target BW. Ad libitum feeding provides a record of the genetic potential for growth which can serve as a benchmark for future studies. The study also allowed for a comparison of ad libitum growth profiles of meat-type pullets and to quantify differences in their sexual maturation timing. Lastly, a photographic record, similar to what was reported in our previous research (Zuidhof et al., 2014), is included in this paper to depict differences in broiler breeder pullet growth over 60 yr under feed restricted and ab libitum feeding conditions.

## MATERIALS AND METHODS

### Animal Care and Use

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 (CCAC, 2009).

### Experimental Design

The study was a 4 × 2 factorial arrangement of treatments with 4 strains of random-bred broiler breeders representing genetics from 1957, 1978, 1995, and 2015, fed either ad libitum or restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains (Aviagen, 2011; Cobb, 2013). From 0 to 19.4 wk birds were reared in floor pens with pine shavings. Pen was the experimental unit. From 19.4 wk onward, birds were individually fed and considered as the experimental unit.

## Stocks

Four random-bred populations were used in the current study, representing commercial broiler lines from 1957, 1978, 1995, and 2015. The current experiment included 2 University of Alberta Meat Control strains unselected since 1957 and 1978 (AMC-1957 and AMC-1978, respectively). The origins of the AMC-1957 and AMC-1978 were described by Zuidhof et al. (2014). The 1995 Random-bred (1995RB) and the 2015 Random-bred (2015RB) strains originated from the University of Arkansas. The 1995RB population was formed as a balanced composite of 7 male (Avian 89, Ross SP, Hubbard HI-Y, Case, Cobb 500, Peterson Regular and Shaver) and 6 female (Cobb 500, Ross 508, Arbor Acres Classic, Hubbard HI-Y, Case 573 and Shaver Yield B) commercial parent stock lines (Harford et al., 2014). The 2015RB population was established through a mating scheme that provided balanced contribution from 4 commercially relevant broiler lines; Cobb MX × Cobb 500, Ross 544 × Ross 308, Ross Yield+ × Ross 708, and the Hubbard HiY line. These populations accounted for 95% of US broiler sales in 2015 (Orlowski et al., 2020). Each of these meat control strains have been maintained without selection since their respective foundational population was established.

## Management

Hatching eggs from the University of Arkansas 1995RB and 2015RB strains were shipped via commercial transport to Edmonton, AB, Canada. A total of 356 eggs from the 1995RB strain and 360 eggs from each of the AMC-1957, AMC-1978 and 2015RB strains were incubated simultaneously at the Alberta Hatching Egg Producers Hatchery at the University of Alberta. The source flock age for the AMC-1957 and AMC-1978 was 57 wk; the source flock age for the 1995RB and 2015RB strains was 55 wk. Eggs were stored for a maximum of 21 d.

Female chicks were neck-tagged and individually weighed at hatch. Each chick was vaccinated with infectious laryngotracheitis, Marek's disease, and coccidiosis vaccines by subcutaneous injection. Individual bird BW was recorded weekly. The coefficient of variation for BW was calculated for each pen. The photoschedule was 23L:1D from d 0 to 3 then reduced to 8L:16D from d 3 to 21 wk of age. Pullets were photostimulated at wk 22 by increasing the photoperiod to 14L:10D in a single step for the remainder of the experiment.

The experiment was conducted from 0 to 29.4 wk of age. From 0 to 3 d of age all pullets were allowed free access to feed in 1 of 4 pens per strain (6.29 $m^2$). The number of birds per pen varied (86, 116, 91, and 123 chicks for AMC-1957, AMC-1978, 1995RB, and 2015RB strains, respectively) based on hatchability. At 3 d of age, pullets were randomly assigned to the restricted or ad libitum treatments and placed in 1 of 2 pens per strain × treatment combination. Hatchability varied between strains and all birds not exhibiting obvious defects were assigned to a feeding treatment. Maximum pen density (kg/$m^2$) is summarized in Table 1. At 19.4 wk, pullets were housed in a 2-tier battery cage system with 1 bird in each of 283 cages (48 × 43 × 41 cm for width, depth, and height, respectively) in an environmentally-controlled facility (summarized in Table 1). For all treatment combinations with the exception of the 1995RB, 16 birds were randomly assigned to the first dissection and 20 birds were randomly assigned the second dissection per strain by treatment combination at the start of the experiment. Due to mortality and lower numbers at the start of the trial, fewer 1995RB were transferred to cages. At the first dissection, some of the second dissection's birds were accidentally removed from cages and were added to the first dissection totals. In addition, some birds reached sexual maturity prior to moving to the cages; these are included in the second dissection totals. Due to mortality during the caged period (after 19.4 wk),

**Table 1.** Total number of birds per treatment × strain combination at 0.4 and 19.4 wk, maximum density at 19.4 wk, and number of birds in each sexual maturation phases[1].

| | Strain[2] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | AMC-1957 | | AMC-1978 | | 1995RB | | 2015RB | |
| | Ad lib | Restricted[3] | Ad lib | Restricted | Ad lib | Restricted | Ad lib | Restricted |
| 0.4 wk (n) | 40 | 41 | 58 | 57 | 44 | 44 | 59 | 57 |
| 19.4 wk (n) | 38 | 39 | 51 | 55 | 33 | 34 | 42 | 49 |
| Maximum pen density (kg/$m^2$) | 4.56 | 4.48 | 12.69 | 7.67 | 12.75 | 4.75 | 22.35 | 6.96 |
| 1st dissection (n) | 16 | 17 | 18 | 18 | 18 | 17 | 17 | 18 |
| 2nd dissection (n) | 18 | 22 | 20 | 18 | 14 | 16 | 18 | 18 |

[1]1st dissection was the dissection at photostimulation time and 2nd dissection was the dissection after second egg.
[2]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.
[3]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

Table 1 represents the actual number of birds that were dissected at each dissection time.

From placement to 3 wk of age, pullets were fed a standard commercial-type broiler breeder starter diet containing 2,921 kcal/kg ME, 19.3% CP, 1.1% Ca, 0.51% available P, 1.05% lysine, 0.44% methionine and 0.65% methionine + cysteine (amino acids on a digestible basis). The grower diet, fed from 4 to 23 wk of age, contained 2,928 kcal/kg ME, 16.8% CP, 1.0% Ca, 0.48% available P, 0.89% lysine, 0.57% methionine, and 0.75% methionine + cysteine (amino acids on a digestible basis).

Feed restriction to the age-specific target BW curve was initiated when the average BW of birds of each strain reached the target BW; otherwise, no feed restriction was applied. Quantitative feed restriction was achieved by limiting daily feed allocation in order to limit growth to the target BW profile. Adjustments to feed allocation were made weekly based on actual BW data. Water was provided ad libitum throughout the experiment.

## Data Collection

Body weight and feed intake data were recorded weekly. Cumulative feed intake per unit of metabolic BW was calculated for each strain × treatment combination by dividing the total feed intake to each age by the average metabolic BW ($BW^{0.51}$) to that age. At the time of hatch, 4 pullets per strain × treatment combination were randomly selected for an ongoing pictorial record of growth and development. Photos were taken from the frontal and lateral aspects at 5, 8, and 20 wk (Figure 1). The size and scale of the birds in the photographic record was calibrated using ImageJ (Schneider et al., 2012).

Skeletal frame size can be indirectly assessed by measuring shank length (Kwakkel et al., 1998). Shank length and chest width were measured on 21 randomly selected birds either at photostimulation or sexual maturity. Shank length was measured using digital calipers as the distance from the foot pad to the top of the hock joint in legs flexed at 90 degrees from the tibia. Chest width was measured 2.5 cm below clavicle bones at the widest point on the chest. Just prior to dissection, keel length was also measured using digital calipers as the distance between the hypocycloid-clavicular joint to the caudal edge of the sternum.

Pullets were considered sexually mature after the second oviposition. Pullets were euthanized by cervical dislocation and dissected either at photostimulation or sexual maturity. Weights of the pectoralis major and minor muscles, abdominal fat pad (adhering to gizzard and abdominal wall, liver, gastrointestinal tract from 1 cm above crop to the distal end of the colon not including the bursa), ovary, oviduct, oviduct contents, number of post ovulatory follicles, and LYF were measured. Total breast muscle weight was the sum of pectoralis major and pectoralis minor.

## Empirical Models

***BW Model*** The following fixed-effect Gompertz model was used to estimate the mature weight and rate of maturing for ad libitum-fed birds of each strain:

$$BW_t = W_m \times exp^{-exp^{-b\left(t-t_{inf}\right)}}$$

where $BW_t$ was predicted BW (kg) at age t (wk); $W_m$ was mature or asymptotic BW (kg); b was a rate of maturing, and $t_{inf}$ was the age (wk) at maximum growth rate (inflection point). The estimated fixed-effect parameters were Wm, b and $t_{inf}$; these were population-level estimates of mature BW, rate of maturing, and inflection point, respectively, which were estimated using the NLIN procedure of SAS (Version 9.4, 2013, SAS Institute Inc., Cary, NC).

***Analysis of Nonlinear Covariance of Carcass Components*** Carcass components curves were estimated from the dissected birds' data on photostimulation and sexual maturity times for each strain and treatment to predict breast muscle, abdominal fat pad, and liver weights using Huxley's allometric model (Huxley and Teissier, 1936). The model had the form:

$$y = ax^b$$

where y was the weight of the carcass part (g), x was eviscerated BW (g), and a and b were coefficients estimated using the NLIN procedure of SAS (Version 9.4, 2013, SAS Institute Inc.).

***Metabolizable Energy Partitioning Model*** A modeling exercise was conducted to estimate total heat production, which may have contributed to differences in feed efficiency. A nonlinear mixed model (Proc NLMIXED; SAS Institute) was used to estimate pen-level energy partitioning coefficients for the model (Romero et al., 2009b).

$$MEI_i = (a + u)\,W_i^b + c(ADG_i) + \varepsilon_i$$

Where $MEI_i$ was the ME intake (kcal/bird/d) for the $i^{th}$ pen; $W_i$ was the average BW (kg) for the corresponding period; $ADG_i$ was the average daily gain (g/d) corrected for mortality for the same period, and $\varepsilon_i$ was the residual error. The $MEI_i$ was calculated using average daily feed intake corrected for mortality. The coefficients a (maintenance requirement; kcal/d/$kg^b$), b (metabolic BW coefficient), and c (gain requirement; kcal/g) were estimated by the procedure. The random coefficient u ($u \sim N[0, \sigma^2]$) estimated the normally distributed pen-specific deviation from the average maintenance requirement. The maintenance requirement (total heat production; Zuidhof, 2019) was converted to Watts using the conversion factor W = 20.64 kcal/d.

## Statistical Analysis

Analysis of variance was conducted using the MIXED procedure of SAS (Version 9.4, Copyright (c) 2002-2012 by SAS Institute Inc.). Variance due to correlated repeated measures on individual subjects was accounted

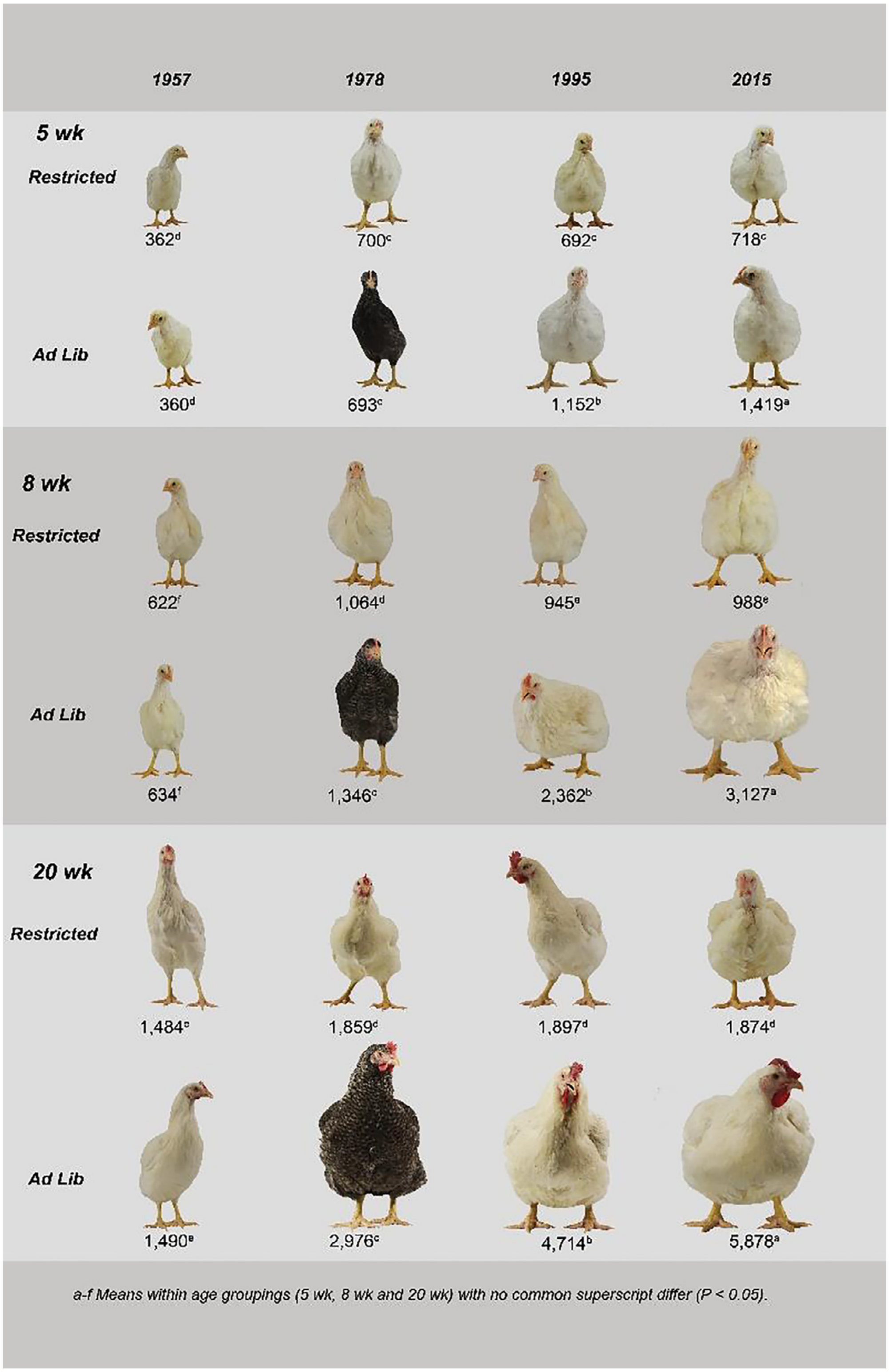


**Figure 1.** Age- and feeding-related changes in size of two University of Alberta Meat Control strains unselected since 1957 and 1978, and two strains originating from the University of Arkansas; 1995 Random-bred and 2015 Random-bred. Within each strain, images are of the same bird at 5, 8, and 20 wk of age. The values under each image indicated BW of each strain at the specified age.

for in the analysis. Subject-specific intercepts were estimated for all variables with repeated observations, and separate variances were estimated for all strain-by-treatment levels. Pairwise Tukey-adjusted differences between means were considered significant where $P \leq 0.05$. Trends or tendencies were discussed where $0.05 < P \leq 0.10$.

## RESULTS AND DISCUSSION

### Growth and Development

***Body Weight*** Although the maternal age across strains was similar, chick hatch BW was lowest in the AMC-1957 strain and highest in the 2015RB strain ($P < 0.001$, Table 2). The BW of 1995RB and 2015RB strains at 2.4

**Table 2.** Body weight of pullets from unselected broiler strains[1] (S) on ad libitum or restricted[2] feed intake treatments (T), from 0 to 22 wk of age.

| Treatment | Restricted | | | | | | | | Ad lib | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Strain | AMC-1957 | | AMC-1978 | | 1995RB | | 2015RB | | AMC-1957 | | AMC-1978 | | 1995RB | | 2015RB | | | | |
| Age (wk) | BW | SEM | BW | SEM | BW | SEM | BW | SEM | BW | SEM | BW | SEM | BW | SEM | BW | SEM | S | T | T x S |
| | g | | | | | | | | | | | | | | | | Probability | | |
| 0.0 | 35$^{c}$ | 0.5 | 40$^{b}$ | 0.5 | 40$^{b}$ | 0.6 | 43$^{a}$ | 0.6 | 35$^{c}$ | 0.5 | 40$^{b}$ | 0.5 | 40$^{b}$ | 0.6 | 44$^{a}$ | 0.5 | < 0.001 | 0.78 | 0.81 |
| 1.4 | 84$^{d}$ | 1.3 | 113$^{c}$ | 1.6 | 133$^{b}$ | 2.9 | 154$^{a}$ | 2.8 | 84$^{d}$ | 1.5 | 114$^{c}$ | 1.5 | 132$^{b}$ | 3.2 | 158$^{a}$ | 2.4 | < 0.001 | 0.64 | 0.79 |
| 2.4 | 141$^{d}$ | 2.2 | 219$^{c}$ | 3.3 | 287$^{b}$ | 6.7 | 319$^{a}$ | 6.9 | 140$^{d}$ | 2.8 | 220$^{c}$ | 3.2 | 275$^{b}$ | 7.1 | 334$^{a}$ | 6.7 | < 0.001 | 0.75 | 0.30 |
| 3.4 | 201$^{d}$ | 3.1 | 342$^{c}$ | 4.7 | 462$^{b}$ | 9.5 | 485$^{b}$ | 11 | 197$^{d}$ | 4.2 | 345$^{c}$ | 5.3 | 497$^{b}$ | 14 | 622$^{a}$ | 14 | < 0.001 | < 0.001 | < 0.001 |
| 4.4 | 288$^{e}$ | 5.1 | 512$^{d}$ | 7.6 | 581$^{c}$ | 11 | 607$^{c}$ | 15 | 289$^{e}$ | 6.2 | 527$^{d}$ | 8.4 | 835$^{b}$ | 23 | 1,007$^{a}$ | 23 | < 0.001 | < 0.001 | < 0.001 |
| 5.4 | 362$^{d}$ | 6.2 | 700$^{c}$ | 9.5 | 692$^{c}$ | 14 | 718$^{c}$ | 17 | 360$^{d}$ | 8.0 | 693$^{c}$ | 11 | 1,152$^{b}$ | 32 | 1,419$^{a}$ | 36 | < 0.001 | < 0.001 | < 0.001 |
| 6.4 | 447$^{f}$ | 7.6 | 872$^{c}$ | 11 | 778$^{e}$ | 15 | 807$^{de}$ | 18 | 449$^{f}$ | 9.7 | 865$^{cd}$ | 15 | 1,566$^{b}$ | 39 | 1,953$^{a}$ | 49 | < 0.001 | < 0.001 | < 0.001 |
| 7.4 | 521$^{f}$ | 9.2 | 990$^{d}$ | 11 | 831$^{e}$ | 18 | 862$^{e}$ | 21 | 511$^{f}$ | 12 | 1,080$^{c}$ | 16 | 1,901$^{b}$ | 46 | 2,496$^{a}$ | 63 | < 0.001 | < 0.001 | < 0.001 |
| 8.4 | 622$^{f}$ | 12 | 1,064$^{d}$ | 11 | 945$^{e}$ | 20 | 988$^{e}$ | 20 | 634$^{f}$ | 17 | 1,346$^{c}$ | 18 | 2,362$^{b}$ | 47 | 3,127$^{a}$ | 66 | < 0.001 | < 0.001 | < 0.001 |
| 9.4 | 762$^{e}$ | 12 | 1,122$^{d}$ | 12 | 1,057$^{d}$ | 21 | 1,082$^{d}$ | 21 | 771$^{e}$ | 15 | 1,572$^{c}$ | 20 | 2,718$^{b}$ | 48 | 3,607$^{a}$ | 68 | < 0.001 | < 0.001 | < 0.001 |
| 10.4 | 858$^{e}$ | 13 | 1,169$^{d}$ | 12 | 1,143$^{d}$ | 23 | 1,150$^{d}$ | 21 | 872$^{e}$ | 16 | 1,747$^{c}$ | 22 | 3,001$^{b}$ | 47 | 3,998$^{a}$ | 62 | < 0.001 | < 0.001 | < 0.001 |
| 11.4 | 960$^{e}$ | 14 | 1,222$^{d}$ | 13 | 1,265$^{d}$ | 28 | 1,215$^{d}$ | 22 | 980$^{e}$ | 17 | 1,901$^{c}$ | 24 | 3,296$^{b}$ | 50 | 4,409$^{a}$ | 61 | < 0.001 | < 0.001 | < 0.001 |
| 12.4 | 1,049$^{e}$ | 16 | 1,269$^{d}$ | 13 | 1,294$^{d}$ | 28 | 1,271$^{d}$ | 20 | 1,069$^{e}$ | 18 | 2,024$^{c}$ | 25 | 3,534$^{b}$ | 63 | 4,709$^{a}$ | 66 | < 0.001 | < 0.001 | < 0.001 |
| 13.4 | 1,127$^{e}$ | 17 | 1,307$^{d}$ | 13 | 1,354$^{d}$ | 28 | 1,356$^{d}$ | 22 | 1,148$^{e}$ | 18 | 2,148$^{c}$ | 28 | 3,739$^{b}$ | 56 | 5,059$^{a}$ | 64 | < 0.001 | < 0.001 | < 0.001 |
| 14.4 | 1,170$^{e}$ | 19 | 1,368$^{d}$ | 13 | 1,400$^{d}$ | 29 | 1,442$^{d}$ | 24 | 1,206$^{e}$ | 19 | 2,264$^{c}$ | 30 | 3,944$^{b}$ | 60 | 5,286$^{a}$ | 71 | < 0.001 | < 0.001 | < 0.001 |
| 15.4 | 1,238$^{e}$ | 19 | 1,420$^{d}$ | 13 | 1,449$^{d}$ | 30 | 1,496$^{d}$ | 24 | 1,273$^{e}$ | 18 | 2,347$^{c}$ | 34 | 4,127$^{b}$ | 59 | 5,543$^{a}$ | 75 | < 0.001 | < 0.001 | < 0.001 |
| 16.4 | 1,274$^{e}$ | 20 | 1,488$^{d}$ | 14 | 1,527$^{d}$ | 31 | 1,528$^{d}$ | 26 | 1,325$^{e}$ | 19 | 2,493$^{c}$ | 35 | 4,275$^{b}$ | 66 | 5,763$^{a}$ | 88 | < 0.001 | < 0.001 | < 0.001 |
| 17.4 | 1,307$^{e}$ | 20 | 1,537$^{d}$ | 16 | 1,579$^{d}$ | 32 | 1,621$^{d}$ | 27 | 1,366$^{e}$ | 20 | 2,609$^{c}$ | 39 | 4,415$^{b}$ | 68 | 5,911$^{a}$ | 99 | < 0.001 | < 0.001 | < 0.001 |
| 18.4 | 1,354$^{e}$ | 21 | 1,627$^{d}$ | 18 | 1,682$^{d}$ | 34 | 1,664$^{d}$ | 30 | 1,418$^{e}$ | 22 | 2,753$^{c}$ | 45 | 4,550$^{b}$ | 67 | 6,048$^{a}$ | 115 | < 0.001 | < 0.001 | < 0.001 |
| 19.4 | 1,408$^{e}$ | 24 | 1,723$^{d}$ | 20 | 1,757$^{d}$ | 36 | 1,750$^{d}$ | 32 | 1,434$^{e}$ | 25 | 2,850$^{c}$ | 47 | 4,717$^{b}$ | 77 | 6,112$^{a}$ | 112 | < 0.001 | < 0.001 | < 0.001 |
| 20.4 | 1,484$^{e}$ | 26 | 1,859$^{d}$ | 24 | 1,897$^{d}$ | 30 | 1,874$^{d}$ | 37 | 1,490$^{e}$ | 33 | 2,976$^{c}$ | 58 | 4,714$^{b}$ | 79 | 5,858$^{a}$ | 133 | < 0.001 | < 0.001 | < 0.001 |
| 21.4 | 1,578$^{e}$ | 34 | 2,033$^{d}$ | 25 | 2,005$^{d}$ | 31 | 2,052$^{d}$ | 41 | 1,600$^{e}$ | 47 | 3,145$^{c}$ | 66 | 4,814$^{b}$ | 58 | 5,879$^{a}$ | 157 | < 0.001 | < 0.001 | < 0.001 |
| 22.4 | 1,655$^{e}$ | 45 | 2,067$^{d}$ | 29 | 2,193$^{d}$ | 35 | 2,163$^{d}$ | 47 | 1,654$^{e}$ | 62 | 3,362$^{c}$ | 136 | 4,734$^{b}$ | 163 | 5,673$^{a}$ | 219 | < 0.001 | < 0.001 | < 0.001 |

$^{a\text{-}f}$Means within row with no common superscript differ ($P < 0.05$).

[1]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

wk was approximately double the BW of AMC-1957, and the BW of the AMC-1978 strain was intermediate. The BW of the AMC-1957 did not reach the BW target curve throughout the trial, therefore, no feed restriction was applied. Feed restriction was initiated at 3 wk for the 1995RB and 2015RB strains and by 3.4 wk the BW of the feed restricted treatments of these modern strains was significantly lower than the BW of the ad libitum treatments. Feed restriction was initiated at 13.4 wk for the AMC-1978 strain. From 8.4 wk to the end of the trial there were no significant differences in BW of the restricted AMC-1978, 1995RB, and 2015RB strains which were all heavier than the AMC-1957 strain. Zuidhof et al. (2014) found that the BW of the 2005 broiler (Ross 308) was 4 times that of the AMC-1957 strain at 7.4 wk. The BW of the 2015RB pullets in this study quadrupled the BW of the AMC-1957 pullets by 5.4 wk.

To enable monitoring for age at the first oviposition as an indicator of sexual maturity, birds were relocated from a pen environment and individually caged at 19.4 wk. During this time all strains maintained or gained weight except the 2015RB strain which lost 254 g BW from 19.4 to 20.4 wk (Table 2). It is possible that in the current study, cages were more confining for the 2015RB strain with a larger frame size and heavier weight compared to other strains. At 22.4 wk of age, BW of restricted-fed AMC-1957, AMC-1978, 1995RB, and 2015RB strains reached 100, 61, 46, and 38% of their ad libitum-fed counterparts, respectively (Table 2). The increasing level of feed restriction in modern broiler breeders over the past decades has increased the gap between potential and target BW in modern broiler breeders. Severe feed restriction raises welfare concerns and causes suboptimal reproductive performance in broiler breeders (van der Klein et al., 2018a,b; Riber et al., 2021). Relaxing growth restriction by increasing prepubertal BW gain by 10% along with advancing the pubertal growth inflection by 15 or 20% resulted in greater margin over feed and pullet cost compared to the breeder-recommended growth trajectory (Afrouziyeh, 2021a). Thus, reducing the severity of feed restriction by increasing target BW in modern broiler breeders seems logical.

***Growth Parameters*** The Gompertz growth model predicted mature weights (Wm) of 1.897, 3.376, 5.021, and 6.672 kg for ad libitum-fed birds of the AMC-1957, AMC-1978, 1995RB, and 2015RB strains, respectively. There was a 3.5-fold increase in mature weight from 1957 to 2015. Rate of maturing (b) increased by 147% and age at maximum growth rate ($t_{inf}$) decreased from 8.81 to 7.35 wk with selection over the last 60 yr (Table 3 and Figure 2). The predicted growth parameters can be used in designing new growth trajectories and age-specific target BW to decrease the severity of feed restriction in modern broiler breeders (Zuidhof, 2020).

## *Feed Intake*

***Actual Feed Intake*** There was a treatment × strain × age interaction for feed intake ($P < 0.001$; Table 4). From 0 to 1.4 wk of age, there were no treatment or strain effects on feed intake. From 2.4 to 22.4 wk of age, feed restriction had no impact on feed intake of the AMC-1957 birds. This was not surprising, as this strain did not achieve the target growth rate, and therefore, birds in both the restricted and ad libitum groups had free access to feed. Feed intake of the AMC-1978 birds was not different between the restricted and ad libitum groups up to 5.4 wk of age. From 6.4 wk of age to the end of the trial, the ad libitum birds consumed a greater amount of feed than the respective restricted birds. Among the 1995RB birds, it was necessary to implement feed restriction beginning at 3.4 wk of age to maintain target growth rates; in the 1995RB strain, feed intake was greater for ad libitum birds than restricted birds from 4.4 wk of age to the end of the trial ($P < 0.001$, Table 4). Feed restriction of the 2015RB birds was implemented at 2.4 wk of age, resulting in greater feed intake of the ad libitum birds compared to the restricted birds from 3.4 wk of age to the end of the trial.

**Table 3.** Parameter estimates for nonlinear mixed Gompertz growth model[1] for broiler breeder strains[2].

| | Growth model parameters | | |
|---|---|---|---|
| Strain | $W_m$, kg | b | $t_{inf}$, wk |
| AMC-1957 | 1.897 | 0.1483 | 8.81 |
| AMC-1978 | 3.376 | 0.1623 | 8.23 |
| 1995RB | 5.021 | 0.2078 | 7.27 |
| 2015RB | 6.672 | 0.2181 | 7.35 |

[1]The nonlinear mixed model was of the form $BW_t = W_m \times exp^{-exp^{-b(t-t_{inf})}}$ where $BW_t$ was predicted BW (kg) at age t (wk); $W_m$ was mature or asymptotic BW (kg); b was a rate of maturing, and $t_{inf}$ was the age (wk) at maximum growth rate (inflection point). The estimated fixed-effect parameters were Wm, b and $t_{inf}$; these were population-level estimates of mature BW, rate of maturing, and inflection point, respectively.

[2]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

From 5.4 wk of age to 13.4 wk of age, feed disappearance for the restricted and ad libitum AMC-1957 birds was extremely high relative to the values before and after this period. It appeared that this strain of birds was particularly prone to wasting feed, and feed that disappeared from the feeder likely accumulated in the litter (Havenstein et al., 2003a,b; Zuidhof et al., 2014). Over time, the relatively smaller values for feed disappearance after 13.4 wk of age likely reflected the consumption of a substantial, but unquantified amount of feed from the litter in addition to that consumed directly from the feeders. This is supported by the fact that from 14.4 to 18.4 wk, the feed disappearance from the feeders would have provided less than the maintenance energy requirements of the birds, and since growth remained positive (Table 2), the birds must have been consuming feed from a source other than the feeder. This did not seem to be an issue for the other strains.

***Relative Feed Intake*** During the rearing phase, the amount of feed allocation to maintain restricted-fed birds on target BW was 24.9, 29.5, 57, and 99.4% of that of their ad libitum-fed counterparts for 2015RB, 1995RB, AMC-1978, and AMC-1957 strains,

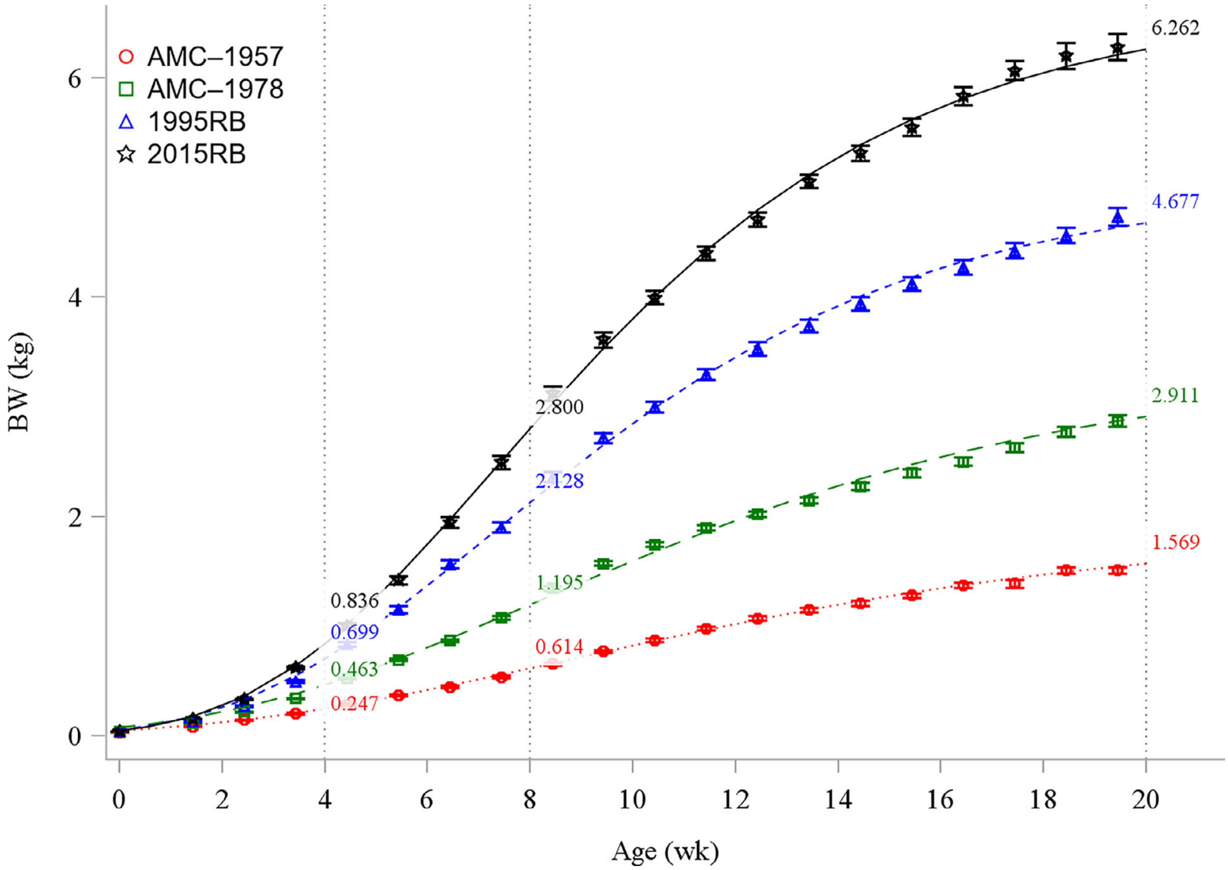


**Figure 2.** Predicted BW of ad libitum fed pullets from University of Alberta Meat Control (AMC) strains unselected since 1957 and 1978, and 1995 Random Bred (1995RB) and the 2015 Random Bred (2015RB) strains originated from the University of Arkansas, showing predicted BW at 4, 8, and 20 wk of age.

respectively (Table 5). When feed intake of restricted birds within each strain was compared to that of the respective ad libitum-fed birds, the degree of restriction was greatest for the 1995RB and 2015RB birds, although interestingly, the additional 20 yr of genetic selection for growth (2015RB vs. 1995RB) did not result in further significant increases in the severity of restriction on a weekly (Table 5) and cumulative (Table 6) basis. As noted previously, feed intake of the AMC-1957 restricted and ad libitum birds was not different, reflecting no feed restriction being applied. The degree of feed restriction in the AMC-1978 birds was intermediate to that of the AMC-1957 birds, and the 1995RB and 2015RB birds. This shows that the degree of feed restriction has been increasing over the past 60 yr in broiler breeders.

Furthermore, cumulative feed intake per unit of metabolic BW in the feed restricted birds, as a percentage of their ad libitum-fed counterparts, was lower for the 1995RB and 2015RB strains compared to AMC-1957 and AMC-1978 strains (Figure 3). Feed restriction is most severe in broiler breeders during the rearing period. The amount of feed allocated from 10 to 16 wk of age is approximately one quarter of what ad libitum-fed individuals eat (Savory et al., 1996; de Jong et al., 2002; Arrazola et al., 2019). Recent studies also suggest that the intensity of feed restriction level has increased in modern commercial broiler breeders, which raises welfare, and more recently, reproductive performance concerns (Mench, 2002; D'Eath et al., 2009; van Krimpen and de Jong, 2014; Tolkamp and D'Eath, 2016; Afrouziyeh et al., 2021b; Zukiwsky et al., 2021). In fact, excessively-restricted modern broiler breeders did not have enough body fat reserves to commence sexual maturity (van Emous et al., 2015; van der Klein et al., 2018a,b; Zuidhof, 2018). Relaxed feed restriction is a logical approach to reduce the intensity of feed restriction in broiler breeders, which could alleviate both welfare and productivity concerns in underfed modern broiler breeders (Hocking et al., 2002; Bruggeman et al., 2005; Zuidhof, 2018; Afrouziyeh et al., 2021b; Zukiwsky et al., 2021).

## Energy Efficiency

The model for predicting ME intake in broiler breeders had the following form:

$$MEI_i = (144.64 + u)\,W_i^{0.51} + 3.98(ADG_i) + \varepsilon_i$$

$$u \sim N\left[0, \sigma_u^2\right]; \sigma_u = 44.75$$

$$\varepsilon \sim N\left[0, \sigma_\varepsilon^2\right]; \sigma_\varepsilon = 55.82$$

In the current study, total heat production or daily maintenance ME requirement for the birds was 145 kcal per kg of metabolic BW ($kg^{0.51}$). The SD of the

**Table 4.** Feed intake[1] of pullets from unselected broiler strains[2] (S) on ad libitum or restricted[3] feed intake treatments (T), from 0 to 20 wk of age.

| | Restricted | | | | | | | | Ad lib | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age (wk) | AMC-1957 | SEM | AMC-1978 | SEM | 1995RB | SEM | 2015RB | SEM | AMC-1957 | SEM | AMC-1978 | SEM | 1995RB | SEM | 2015RB | SEM |
| | Feed intake (g/d) | | | | | | | | | | | | | | | |
| 0.6 | 8 | 5.7 | 8 | 5.7 | 10 | 5.7 | 10 | 5.7 | 8 | 5.7 | 9 | 5.7 | 11 | 5.7 | 10 | 5.7 |
| 1.4 | 12 | 4.1 | 17 | 4.0 | 21 | 4.0 | 19 | 4.1 | 10 | 4.1 | 16 | 4.1 | 19 | 4.3 | 21 | 4.0 |
| 2.4 | 31$^{ab}$ | 4.0 | 36$^{ab}$ | 4.5 | 44$^{ab}$ | 4.1 | 47$^{ab}$ | 4.3 | 24$^{b}$ | 4.4 | 37$^{ab}$ | 5.1 | 54$^{a}$ | 4.1 | 44$^{ab}$ | 4.6 |
| 3.4 | 36$^{bc}$ | 4.8 | 37$^{bc}$ | 4.0 | 46$^{bc}$ | 4.0 | 46$^{bc}$ | 4.0 | 26$^{c}$ | 4.0 | 43$^{bc}$ | 4.1 | 65$^{ab}$ | 7.4 | 77$^{a}$ | 4.6 |
| 4.4 | 58$^{bc}$ | 5.2 | 64$^{bc}$ | 4.3 | 46$^{c}$ | 5.7 | 46$^{c}$ | 4.0 | 50$^{c}$ | 4.1 | 85$^{b}$ | 4.5 | 131$^{a}$ | 5.2 | 120$^{a}$ | 4.6 |
| 5.4 | 78$^{bc}$ | 9.3 | 81$^{b}$ | 4.6 | 46$^{c}$ | 5.7 | 46$^{c}$ | 5.7 | 73$^{bc}$ | 6.4 | 102$^{b}$ | 4.3 | 150$^{a}$ | 8.9 | 169$^{a}$ | 4.1 |
| 6.4 | 107$^{bc}$ | 7.1 | 79$^{cd}$ | 4.9 | 46$^{e}$ | 4.0 | 46$^{de}$ | 5.7 | 95$^{bcd}$ | 9.2 | 116$^{b}$ | 4.1 | 167$^{a}$ | 9.5 | 203$^{a}$ | 4.3 |
| 7.4 | 83$^{cd}$ | 10.6 | 71$^{d}$ | 4.5 | 46$^{d}$ | 4.0 | 46$^{d}$ | 5.7 | 112$^{c}$ | 4.2 | 110$^{c}$ | 4.2 | 158$^{b}$ | 4.2 | 220$^{a}$ | 4.1 |
| 8.4 | 103$^{cd}$ | 13.2 | 51$^{d}$ | 4.3 | 46$^{d}$ | 5.7 | 46$^{d}$ | 5.7 | 96$^{c}$ | 5.0 | 113$^{c}$ | 6.6 | 173$^{b}$ | 4.1 | 243$^{a}$ | 4.1 |
| 9.4 | 125$^{bcd}$ | 16.8 | 49$^{d}$ | 4.2 | 48$^{d}$ | 4.0 | 46$^{d}$ | 4.0 | 111$^{c}$ | 4.5 | 114$^{c}$ | 5.1 | 181$^{b}$ | 4.3 | 235$^{a}$ | 4.1 |
| 10.4 | 125$^{bc}$ | 14.8 | 48$^{d}$ | 4.1 | 43$^{d}$ | 4.0 | 43$^{d}$ | 4.0 | 126$^{c}$ | 7.7 | 104$^{c}$ | 4.0 | 182$^{ab}$ | 5.4 | 225$^{a}$ | 8.3 |
| 11.4 | 96$^{c}$ | 5.5 | 48$^{d}$ | 4.1 | 41$^{d}$ | 4.2 | 41$^{d}$ | 4.0 | 99$^{c}$ | 4.4 | 96$^{c}$ | 4.5 | 195$^{b}$ | 4.3 | 229$^{a}$ | 4.9 |
| 12.4 | 119$^{b}$ | 9.0 | 48$^{c}$ | 4.1 | 45$^{c}$ | 4.8 | 42$^{c}$ | 4.1 | 130$^{b}$ | 14.2 | 91$^{b}$ | 4.4 | 209$^{a}$ | 4.1 | 231$^{a}$ | 6.3 |
| 13.4 | 71$^{cd}$ | 4.6 | 49$^{cd}$ | 4.0 | 44$^{d}$ | 4.2 | 43$^{d}$ | 4.1 | 80$^{bc}$ | 6.0 | 104$^{b}$ | 5.2 | 203$^{a}$ | 4.0 | 229$^{a}$ | 7.3 |
| 14.4 | 57$^{c}$ | 5.6 | 52$^{c}$ | 4.1 | 43$^{c}$ | 4.1 | 45$^{c}$ | 4.5 | 70$^{c}$ | 5.6 | 118$^{b}$ | 4.1 | 210$^{a}$ | 4.7 | 222$^{a}$ | 10.1 |
| 15.4 | 50$^{c}$ | 4.0 | 55$^{c}$ | 4.1 | 46$^{c}$ | 4.1 | 45$^{c}$ | 4.1 | 52$^{c}$ | 4.1 | 115$^{b}$ | 6.1 | 196$^{a}$ | 9.2 | 228$^{a}$ | 13.9 |
| 16.4 | 42$^{c}$ | 4.6 | 62$^{c}$ | 4.2 | 51$^{c}$ | 4.3 | 48$^{c}$ | 4.1 | 41$^{c}$ | 4.1 | 119$^{b}$ | 4.1 | 195$^{a}$ | 4.2 | 218$^{a}$ | 7.2 |
| 17.4 | 36$^{c}$ | 6.0 | 66$^{c}$ | 4.4 | 56$^{c}$ | 4.4 | 56$^{c}$ | 5.7 | 40$^{c}$ | 4.3 | 124$^{b}$ | 4.3 | 188$^{a}$ | 4.1 | 209$^{a}$ | 11.6 |
| 18.4 | 40$^{d}$ | 5.5 | 75$^{c}$ | 4.1 | 65$^{cd}$ | 4.7 | 60$^{cd}$ | 4.0 | 43$^{d}$ | 4.2 | 133$^{b}$ | 5.9 | 182$^{a}$ | 4.0 | 204$^{a}$ | 5.9 |
| 19.4 | 51$^{cd}$ | 9.5 | 77$^{c}$ | 4.1 | 67$^{cd}$ | 4.8 | 60$^{cd}$ | 4.0 | 48$^{d}$ | 4.2 | 127$^{b}$ | 4.1 | 172$^{a}$ | 4.5 | 182$^{ab}$ | 11.3 |
| Source of variation | Probability | | | | | | | | | | | | | | | |
| T | < 0.001 | | | | | | | | | | | | | | | |
| S | < 0.001 | | | | | | | | | | | | | | | |
| T × S | < 0.001 | | | | | | | | | | | | | | | |
| Age | < 0.001 | | | | | | | | | | | | | | | |
| T × Age | < 0.001 | | | | | | | | | | | | | | | |
| S× Age | < 0.001 | | | | | | | | | | | | | | | |
| T × S × Age | < 0.001 | | | | | | | | | | | | | | | |

[a-e]Means within row with no common superscript differ ($P < 0.05$).

[1]Pen feed intake was divided by the total number of bird-days for the week (calculated by adding the number of birds in the pen on each day to adjust for mortality) to calculate average daily feed intake per bird.

[2]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[3]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

**Table 5.** Daily feed intake[1] of feed restricted[2] birds, as a percentage of ad libitum intake of birds of the same unselected broiler strains[3].

| | Strain | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Age | AMC-1957 | SEM | AMC-1978 | SEM | 1995RB | SEM | 2015RB | SEM |
| Wk | Feed intake (% of ad libitum, within strain) | | | | | | | |
| 0 to 0.6 | 100.0 | 5.9 | 100.0 | 5.9 | 100.0 | 5.9 | 100.0 | 5.9 |
| 0.6 to 1.4 | 114.9 | 5.7 | 105.3 | 4.5 | 112.8 | 4.2 | 93.0 | 4.6 |
| 1.4 to 2.4 | 129.1[a] | 4.2 | 96.8[ab] | 6.4 | 82.9[b] | 4.4 | 106.1[ab] | 5.1 |
| 2.4 to 3.4 | 135.9[a] | 10.1 | 86.1[b] | 4.2 | 70.2[bc] | 4.2 | 59.1[c] | 4.2 |
| 3.4 to 4.4 | 116.6[a] | 7.3 | 75.4[b] | 4.4 | 35.1[c] | 5.9 | 38.1[c] | 4.2 |
| 4.4 to 5.4 | 107.0[a] | 11.3 | 79.3[a] | 4.6 | 30.7[b] | 5.9 | 27.2[b] | 5.9 |
| 5.4 to 6.4 | 113.5[a] | 7.0 | 68.1[b] | 4.7 | 27.7[c] | 4.2 | 22.7[c] | 5.9 |
| 6.4 to 7.4 | 74.0[a] | 9.0 | 64.1[a] | 4.5 | 29.3[b] | 4.2 | 20.9[b] | 5.9 |
| 7.4 to 8.4 | 106.8[a] | 12.7 | 45.0[b] | 4.3 | 26.5[b] | 5.9 | 18.9[b] | 5.9 |
| 8.4 to 9.4 | 112.4[a] | 14.1 | 43.1[b] | 4.2 | 26.7[b] | 4.2 | 19.7[b] | 4.2 |
| 9.4 to 10.4 | 98.9[a] | 11.1 | 46.3[b] | 4.2 | 23.4[bc] | 4.2 | 19.1[c] | 4.2 |
| 10.4 to 11.4 | 96.6[a] | 5.4 | 49.7[b] | 4.2 | 20.7[c] | 4.2 | 18.1[c] | 4.2 |
| 11.4 to 12.4 | 91.7[a] | 7.0 | 52.8[b] | 4.2 | 21.3[c] | 4.3 | 18.2[c] | 4.2 |
| 12.4 to 13.4 | 89.2[a] | 4.9 | 46.7[b] | 4.2 | 21.5[bc] | 4.2 | 18.8[c] | 4.2 |
| 13.4 to 14.4 | 82.4[a] | 6.6 | 44.0[b] | 4.2 | 20.7[b] | 4.2 | 20.5[b] | 4.2 |
| 14.4 to 15.4 | 95.7[a] | 4.2 | 48.0[b] | 4.2 | 23.7[bc] | 4.2 | 19.6[c] | 4.2 |
| 15.4 to 16.4 | 102.0[a] | 6.3 | 51.7[b] | 4.2 | 26.4[bc] | 4.2 | 22.2[c] | 4.2 |
| 16.4 to 17.4 | 90.7[a] | 10.9 | 53.0[ab] | 4.4 | 30.0[b] | 4.3 | 27.1[b] | 5.9 |
| 17.4 to 18.4 | 91.9[a] | 9.0 | 56.6[ab] | 4.2 | 35.8[bc] | 4.3 | 29.4[c] | 4.2 |
| 18.4 to 19.4 | 105.0[ab] | 16.9 | 60.8[a] | 4.2 | 38.6[ab] | 4.4 | 33.1[b] | 4.2 |
| Source of variation | Probability | | | | | | | |
| Age | < 0.001 | | | | | | | |
| Strain | < 0.001 | | | | | | | |
| Strain × Age | < 0.001 | | | | | | | |

[a-c]Means within rows with no common superscript differ ($P < 0.05$).
[1]Pen feed intake was divided by the total number of bird-days for the week (calculated by adding the number of birds in the pen on each day to adjust for mortality) to calculate average daily feed intake per bird.
[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.
[3]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

**Table 6.** Cumulative feed intake[1] of feed restricted birds[2], as a percentage of ad libitum intake of birds of the same unselected broiler strains[3].

| | Strain | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Age | AMC-1957 | SEM | AMC-1978 | SEM | 1995RB | SEM | 2015RB | SEM |
| wk | Feed intake (% of ad libitum, within strain) | | | | | | | |
| 0 to 0.6 | 100.0 | 4.7 | 100.0 | 4.7 | 100.0 | 4.7 | 100.0 | 4.7 |
| 0 to 1.4 | 109.9 | 4.4 | 104.0 | 3.6 | 109.3 | 3.4 | 94.7 | 3.7 |
| 0 to 2.4 | 122.3[a] | 3.6 | 99.2[ab] | 5.2 | 90.6[b] | 3.4 | 102.2[ab] | 4.3 |
| 0 to 3.4 | 128.0[a] | 4.7 | 93.5[b] | 4.0 | 81.2[b] | 3.3 | 79.2[b] | 3.6 |
| 0 to 4.4 | 122.9[a] | 5.8 | 85.2[b] | 3.4 | 59.0[c] | 3.3 | 60.5[c] | 3.4 |
| 0 to 5.4 | 116.7[a] | 8.0 | 83.1[a] | 3.5 | 49.0[b] | 3.3 | 47.5[b] | 3.4 |
| 0 to 6.4 | 115.6[a] | 7.6 | 78.8[a] | 3.6 | 42.9[b] | 3.3 | 39.6[b] | 3.3 |
| 0 to 7.4 | 103.7[a] | 8.1 | 75.6[a] | 3.6 | 40.0[b] | 3.3 | 34.8[b] | 3.3 |
| 0 to 8.4 | 104.4[a] | 9.1 | 70.1[a] | 3.6 | 37.5[b] | 3.3 | 31.3[b] | 3.3 |
| 0 to 9.4 | 105.8[a] | 10.1 | 65.9[a] | 3.6 | 35.7[b] | 3.3 | 29.3[b] | 3.3 |
| 0 to 10.4 | 104.6[a] | 10.4 | 63.5[a] | 3.6 | 34.0[b] | 3.3 | 27.8[b] | 3.3 |
| 0 to 11.4 | 103.7[a] | 9.7 | 62.1[a] | 3.5 | 32.2[b] | 3.3 | 26.6[b] | 3.3 |
| 0 to 12.4 | 102.0[a] | 7.8 | 61.3[b] | 3.5 | 30.9[c] | 3.3 | 25.6[c] | 3.3 |
| 0 to 13.4 | 101.0[a] | 7.5 | 59.9[b] | 3.5 | 29.9[c] | 3.3 | 24.9[c] | 3.3 |
| 0 to 14.4 | 99.9[a] | 7.4 | 58.4[b] | 3.5 | 28.9[c] | 3.3 | 24.5[c] | 3.3 |
| 0 to 15.4 | 99.7[a] | 7.1 | 57.6[b] | 3.4 | 28.5[c] | 3.3 | 24.1[c] | 3.3 |
| 0 to 16.4 | 99.8[a] | 6.8 | 57.1[b] | 3.4 | 28.3[c] | 3.3 | 24.0[c] | 3.3 |
| 0 to 17.4 | 99.5[a] | 6.3 | 56.8[b] | 3.4 | 28.4[c] | 3.3 | 24.2[c] | 3.3 |
| 0 to 18.4 | 99.2[a] | 5.9 | 56.8[b] | 3.3 | 28.9[c] | 3.3 | 24.5[c] | 3.3 |
| 0 to 19.4 | 99.4[a] | 5.3 | 57.0[b] | 3.3 | 29.5[c] | 3.3 | 24.9[c] | 3.3 |
| Source of variation | Probability | | | | | | | |
| Age | < 0.001 | | | | | | | |
| Strain | < 0.001 | | | | | | | |
| Strain × Age | < 0.001 | | | | | | | |

[a-c]Means within rows with no common superscript differ ($P < 0.05$).
[1]Cumulative feed intake was calculated on a per pen basis in which individual periods were summed and corrected for mortality.
[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.
[3]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

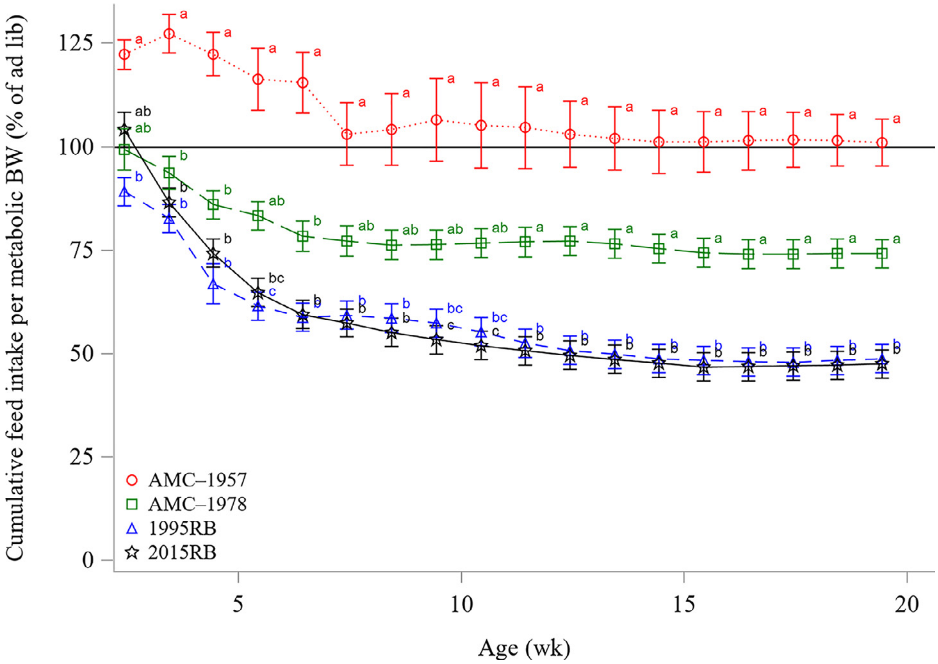


**Figure 3.** Cumulative feed intake per metabolic BW ($BW^{0.51}$) of feed restricted pullets from University of Alberta Meat Control (AMC) strains unselected since 1957 and 1978, and 1995 Random Bred (1995RB) and the 2015 Random Bred (2015RB) strains originated from the University of Arkansas relative to ad libitum fed (———) birds of the same strain. [a-d]Means within age with no common letter differ ($P < 0.05$).

maintenance ME requirement among individual pens was 45 kcal/$kg^{0.51}$. This is in line with previously reported values (21.3 to 58.3 kcal/$kg^{0.54}$) for the SD of broiler breeder maintenance requirement (Romero et al., 2009b). Although heat production estimates with ad libitum feeding were more than 240% higher for the 2015RB strain compared to the AMC-1957 strain (23.9 vs. 9.8 watts for a 2.00 kg 2015RB and AMC-1957 strains, respectively), feed restricted birds in the 1995RB and 2015RB strains had lower heat production relative to the AMC-1957 and AMC-1978 ($P < 0.001$; Table 7). In other words, under restricted feed conditions the 1995RB and 2015RB strains utilized feed more efficiently compared to other strains. This is probably related to the increasing severity of feed restriction over the past 60 yr in broiler breeders and selection pressure on feed efficiency as a contributing factor. Feed restriction increases efficiency by reducing heart rate, blood pressure, and body temperature (Savory et al., 2006). Afrouziyeh et al. (2022b) relaxed broiler breeder feed restriction level through increasing their prepubertal target BW gain by 10% and observed a 1.47 kcal/kg $BW^{0.56}$ increase in residual heat production compared to the standard-restricted birds. The authors hypothesized that more severe feed restriction stimulates physiological mechanisms that reduce heat production.

**Table 7.** Estimated daily maintenance ME requirements, and calculated heat production per bird[1] at 2 and 4 kg.

| | Strain[2] (S) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Treatment (T) | AMC-1957 | SEM | AMC-1978 | SEM | 1995RB | SEM | 2015RB | SEM |
| | | | | kcal/$kg^{0.5}$1/d | | | | |
| Restricted[3] | 140.0[cd] | 11.85 | 110.3[d] | 2.06 | 86.1[e] | 0.86 | 84.5[e] | 0.33 |
| Ad lib | 142.6[c] | 3.07 | 191.3[b] | 3.07 | 312.4[a] | 0.55 | 346.1[a] | 19.44 |
| | | | | kcal/kg/d at 2 kg BW (watts) | | | | |
| Restricted | 100 (9.7 W) | | 79 (7.6 W) | | 61 (5.9 W) | | 60 (5.8 W) | |
| Ad lib | 102 (9.8 W) | | 136 (13.2 W) | | 222 (21.6 W) | | 246 (23.9 W) | |
| | | | | kcal/kg/d at 4 kg BW (watts) | | | | |
| Restricted | n/a | | 56 (10.8 W) | | 44 (8.5 W) | | 43 (8.3 W) | |
| Ad lib | n/a | | 97 (18.8 W) | | 158 (30.7 W) | | 175 (34.0 W) | |
| Source of variation | | | | Probability | | | | |
| T | | | | < 0.001 | | | | |
| S | | | | < 0.001 | | | | |
| T x S | | | | < 0.001 | | | | |

[a-e]Means with no common superscript differ ($P < 0.05$).

[1]Heat production estimates (kcal/kg of BW), converted to watts (1 W = 20.64 kcal/d), and multiplied by 2 or 4 kg of BW to estimate the heat production per animal.

[2]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[3]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

## Carcass Components

Expected weights of carcass parts can be calculated from the nonlinear covariance coefficients presented in Table 8. Relative to AMC-1957 and AMC-1978 strains, breast muscle weight curves were shifted upward in the 1995RB and 2015RB ($P < 0.001$, Figure 4). Genetic selection in the last 4 decades has prioritized selection for growth and meat yield. Breast yield on a percent BW basis was not affected by feed restriction in any of the lines (Table 9).

Abdominal fat pad weight curves were shifted downward in the 1995RB and 2015RB compared to those in AMC-1957 and AMC-1978 strains ($P < 0.001$, Figure 5). Furthermore, 2015RB birds had lower abdominal fat pad curve compared to the 1995RB birds ($P < 0.001$); however, there was no difference between the abdominal fat pad curves of the AMC-1957 and AMC-1978 strains. The impact of breeder selection between 1957 and 1978 was mostly on BW. However, there has been a shift in the way the birds prioritize their nutrient deposition since 1978. More specifically, as a result of commercial selection pressure on feed efficiency and growth after 1978, abdominal fat pad decreased and breast muscle weight increased. Thus, modern breeder pullets are leaner compared to the older random-bred strain pullets, and rearing to a similar body weight might have a negative impact on sexual maturation and sustaining egg production (van Emous et al., 2015; van der Klein et al., 2018a,b; Zuidhof, 2018). It has been hypothesized that achieving a critical threshold of body composition and fat during the juvenile stage is required for sexual development (Bornstein et al., 1984; van Emous et al., 2013). Adipose tissue may play an important role in sexual maturation through the effect of adipokines on the hypothalamus pituitary gland axis (reviewed by Hanlon et al., 2020). It was previously shown that carcass fat at sexual maturity was between 11 and 15% of total BW (Joseph et al., 2000; Renema et al., 2007). Afrouziyeh et al. (2021b) reported that the minimum body fat threshold for sexual maturation is below 8% in broiler breeders. van der Klein et al. (2018a) hypothesized that some underfed modern broiler breeders did not have enough body fat reserves to commence sexual maturity. The authors reported that pullets that had not entered lay prior to 55 wk of age had abdominal fat pads which averaged 1.5% of their BW, while fat pads of birds that had entered lay averaged 2.5%, suggesting that a minimum threshold does exist.

Liver weight as a proportion of BW in the 2015RB strain was less than that of in the older strains ($P < 0.001$, Figure 6). At photostimulation, the AMC-1978 had the largest livers in both the feed restricted and ad libitum fed treatments (Table 9). The liver is a major metabolic support organ and is involved in reproduction through role of the liver in fat metabolism (Cieślik et al., 2011; He et al., 2014) and yolk precursor synthesis (Wang et al., 2013; Wood et al., 2021). It can be hypothesized that reduced adipose fat, as well as more severe feed restriction have decreased the metabolic rate in

**Table 8.** Nonlinear covariance coefficients of unselected broiler breeder strains[1].

| Strain[2] | AMC-1957 | | | | AMC-1978 | | | | 1995RB | | | | 2015RB | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment[3] | Ad lib | | Restricted | | Ad lib | | Restricted | | Ad lib | | Restricted | | Ad lib | | Restricted | |
| | Nonlinear covariance coefficients | | | | | | | | | | | | | | | |
| Carcass component | a | b | a | b | a | b | a | b | a | b | a | b | a | b | a | b |
| Breast | 0.1722 | 0.976 | 0.1971 | 0.961 | 0.2997 | 0.911 | 2.7586 | 0.62 | 0.0267 | 1.21 | 0.6754 | 0.829 | 0.5293 | 0.905 | 0.0206 | 1.304 |
| Fat pad | 23E-9 | 2.858 | 66E-10 | 3.028 | 0.0367 | 1.071 | 242E-8 | 2.232 | 0.0249 | 1.119 | 771E-9 | 2.321 | 131E-7 | 1.945 | 22E-10 | 2.994 |
| Liver | 15E-8 | 2.601 | 715E-9 | 2.403 | 0.0007 | 1.46 | 6E-5 | 1.764 | 516E-8 | 1.968 | 0.0001 | 1.691 | 15E-6 | 1.798 | 0.0522 | 0.844 |

[1]The nonlinear model was of the form $y = ax^b$ where y was the weight of the carcass part (g), x was eviscerated BW (g), and a and b were estimated nonlinear covariance coefficients.

[2]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[3]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

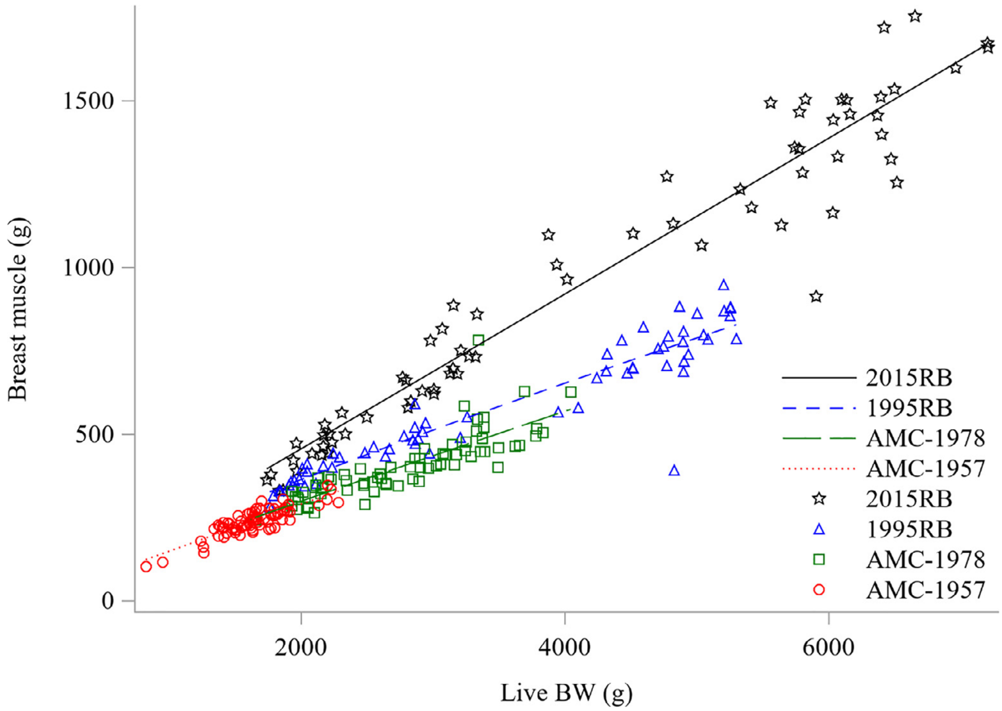


**Figure 4.** Nonlinear covariance curves for breast muscle weight of University of Alberta Meat Control (AMC) strains unselected since 1957 and 1978, and 1995 Random Bred (1995RB) and the 2015 Random Bred (2015RB) strains originated from the University of Arkansas dissected either at photostimulation or sexual maturity.

**Table 9.** Breast, p. major, p. minor, liver and abdominal fat pad yield of pullets from unselected broiler strains[1] on ad libitum or restricted[2] feed intake treatments.

| Fate | Effect | Treatment (T) | Strain (S) | Breast | SEM | P. major | SEM | P. Minor | SEM | Liver | SEM | Fatpad | SEM |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | % of live BW | | | | | | | | | |
| 22 wk (A) | S | | AMC-1957 | 15.2$^{c}$ | 0.23 | 11.3$^{c}$ | 0.19 | 3.9$^{c}$ | 0.07 | 1.9$^{a}$ | 0.08 | 1.9$^{c}$ | 0.13 |
| | | | AMC-1978 | 15.0$^{c}$ | 0.23 | 11.2$^{c}$ | 0.18 | 3.8$^{c}$ | 0.06 | 2.2$^{a}$ | 0.10 | 4.9$^{a}$ | 0.22 |
| | | | 1995RB | 17.3$^{b}$ | 0.18 | 13.1$^{b}$ | 0.16 | 4.2$^{b}$ | 0.05 | 1.6$^{b}$ | 0.06 | 4.4$^{a}$ | 0.19 |
| | | | 2015RB | 22.3$^{a}$ | 0.33 | 17.7$^{a}$ | 0.28 | 4.6$^{a}$ | 0.09 | 1.5$^{b}$ | 0.07 | 2.9$^{b}$ | 0.13 |
| | T | Restricted | | 17.6 | 0.16 | 13.2 | 0.13 | 4.4$^{a}$ | 0.05 | 1.7$^{b}$ | 0.04 | 1.7$^{b}$ | 0.09 |
| | | Ad lib | | 17.3 | 0.19 | 13.4 | 0.16 | 3.9$^{b}$ | 0.05 | 1.9$^{a}$ | 0.07 | 5.3$^{a}$ | 0.15 |
| | S × T | Restricted | AMC-1957 | 15.4$^{cd}$ | 0.26 | 11.4$^{e}$ | 0.22 | 4.0$^{cd}$ | 0.09 | 2.0$^{ab}$ | 0.12 | 1.9$^{cd}$ | 0.21 |
| | | | AMC-1978 | 15.4$^{cd}$ | 0.30 | 11.4$^{e}$ | 0.22 | 4.0$^{cd}$ | 0.10 | 1.8$^{b}$ | 0.06 | 2.8$^{c}$ | 0.22 |
| | | | 1995RB | 18.3$^{b}$ | 0.27 | 13.7$^{c}$ | 0.25 | 4.6$^{b}$ | 0.07 | 1.5$^{c}$ | 0.02 | 1.7$^{d}$ | 0.16 |
| | | | 2015RB | 21.4$^{a}$ | 0.44 | 16.3$^{b}$ | 0.35 | 5.1$^{a}$ | 0.12 | 1.5$^{c}$ | 0.05 | 0.5$^{e}$ | 0.10 |
| | | Ad lib | AMC-1957 | 15.0$^{cd}$ | 0.37 | 11.3$^{e}$ | 0.30 | 3.8$^{cd}$ | 0.12 | 1.8$^{bc}$ | 0.11 | 2.0$^{cd}$ | 0.17 |
| | | | AMC-1978 | 14.6$^{d}$ | 0.36 | 10.9$^{e}$ | 0.28 | 3.7$^{d}$ | 0.08 | 2.5$^{a}$ | 0.19 | 6.9$^{a}$ | 0.38 |
| | | | 1995RB | 16.3$^{c}$ | 0.26 | 12.5$^{d}$ | 0.21 | 3.8$^{cd}$ | 0.07 | 1.7$^{bc}$ | 0.12 | 7.1$^{a}$ | 0.34 |
| | | | 2015RB | 23.2$^{a}$ | 0.49 | 19.0$^{a}$ | 0.44 | 4.2$^{c}$ | 0.13 | 1.5$^{bc}$ | 0.13 | 5.3$^{b}$ | 0.24 |
| Maturity (B) | S | | AMC-1957 | 14.1$^{c}$ | 0.18 | 10.5$^{c}$ | 0.16 | 3.6$^{c}$ | 0.04 | 2.7$^{a}$ | 0.14 | 2.6$^{b}$ | 0.17 |
| | | | AMC-1978 | 14.2$^{c}$ | 0.30 | 10.6$^{c}$ | 0.23 | 3.6$^{c}$ | 0.08 | 2.8$^{a}$ | 0.12 | 5.1$^{a}$ | 0.21 |
| | | | 1995RB | 16.2$^{b}$ | 0.38 | 12.3$^{b}$ | 0.30 | 4.0$^{b}$ | 0.10 | 2.0$^{b}$ | 0.09 | 4.7$^{a}$ | 0.17 |
| | | | 2015RB | 23.5$^{a}$ | 0.40 | 18.7$^{a}$ | 0.34 | 4.8$^{a}$ | 0.10 | 1.5$^{c}$ | 0.05 | 3.2$^{b}$ | 0.14 |
| | T | Restricted | | 17.1 | 0.19 | 13.0 | 0.15 | 4.1$^{a}$ | 0.06 | 2.2 | 0.06 | 2.9$^{b}$ | 0.10 |
| | | Ad lib | | 16.9 | 0.27 | 13.1 | 0.22 | 3.8$^{b}$ | 0.06 | 2.3 | 0.08 | 4.9$^{a}$ | 0.14 |
| | S × T | Restricted | AMC-1957 | 14.4$^{c}$ | 0.21 | 10.7$^{c}$ | 0.17 | 3.7 | 0.06 | 2.6 | 0.17 | 2.5$^{de}$ | 0.22 |
| | | | AMC-1978 | 13.8$^{c}$ | 0.27 | 10.2$^{c}$ | 0.18 | 3.5 | 0.09 | 2.6 | 0.14 | 3.9$^{bc}$ | 0.28 |
| | | | 1995RB | 17.3$^{b}$ | 0.35 | 13.0$^{b}$ | 0.27 | 4.3 | 0.11 | 2.0 | 0.12 | 2.9$^{cd}$ | 0.18 |
| | | | 2015RB | 23.0$^{a}$ | 0.57 | 17.9$^{a}$ | 0.46 | 5.0 | 0.16 | 1.6 | 0.05 | 2.1$^{e}$ | 0.12 |
| | | Ad lib | AMC-1957 | 13.8$^{c}$ | 0.30 | 10.3$^{c}$ | 0.26 | 3.5 | 0.05 | 2.7 | 0.22 | 2.8$^{cde}$ | 0.26 |
| | | | AMC-1978 | 14.6$^{c}$ | 0.54 | 11.0$^{c}$ | 0.41 | 3.6 | 0.14 | 3.0 | 0.19 | 6.2$^{a}$ | 0.31 |
| | | | 1995RB | 15.1$^{bc}$ | 0.67 | 11.5$^{bc}$ | 0.53 | 3.6 | 0.18 | 2.1 | 0.14 | 6.4$^{a}$ | 0.30 |
| | | | 2015RB | 23.9$^{a}$ | 0.57 | 19.5$^{a}$ | 0.50 | 4.5 | 0.11 | 1.4 | 0.09 | 4.2$^{b}$ | 0.24 |
| Fate | Source of variation | | | Probability | | | | | | | | | |
| 22 wk (A) | S | | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | |
| | T | | | 0.14 | | 0.35 | | < 0.001 | | 0.009 | | < 0.001 | |
| | S × T | | | < 0.001 | | < 0.001 | | < 0.001 | | 0.003 | | < 0.001 | |
| Maturity (B) | S | | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | |
| | T | | | 0.44 | | 0.79 | | < 0.001 | | 0.36 | | < 0.001 | |
| | S × T | | | 0.008 | | 0.002 | | 0.023 | | 0.051 | | < 0.001 | |

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

[1]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

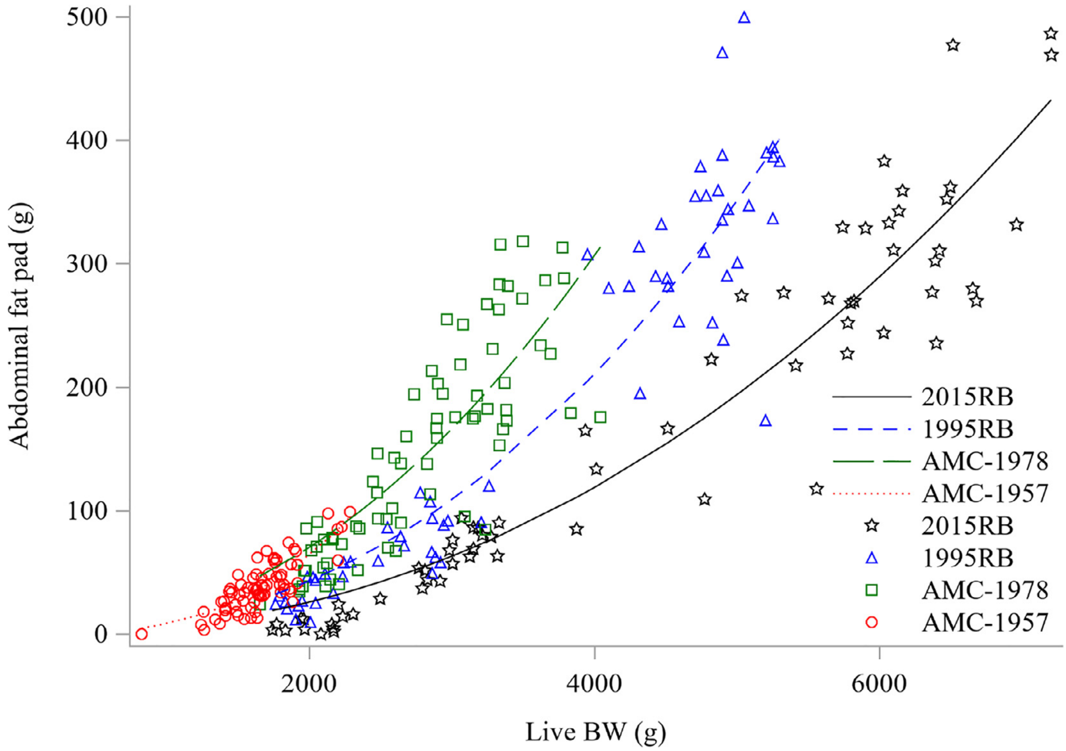


**Figure 5.** Nonlinear covariance curves for abdominal fat pad weight of University of Alberta Meat Control (AMC) strains unselected since 1957 and 1978, and 1995 Random Bred (1995RB) and the 2015 Random Bred (2015RB) strains originated from the University of Arkansas dissected either at photostimulation or sexual maturity.

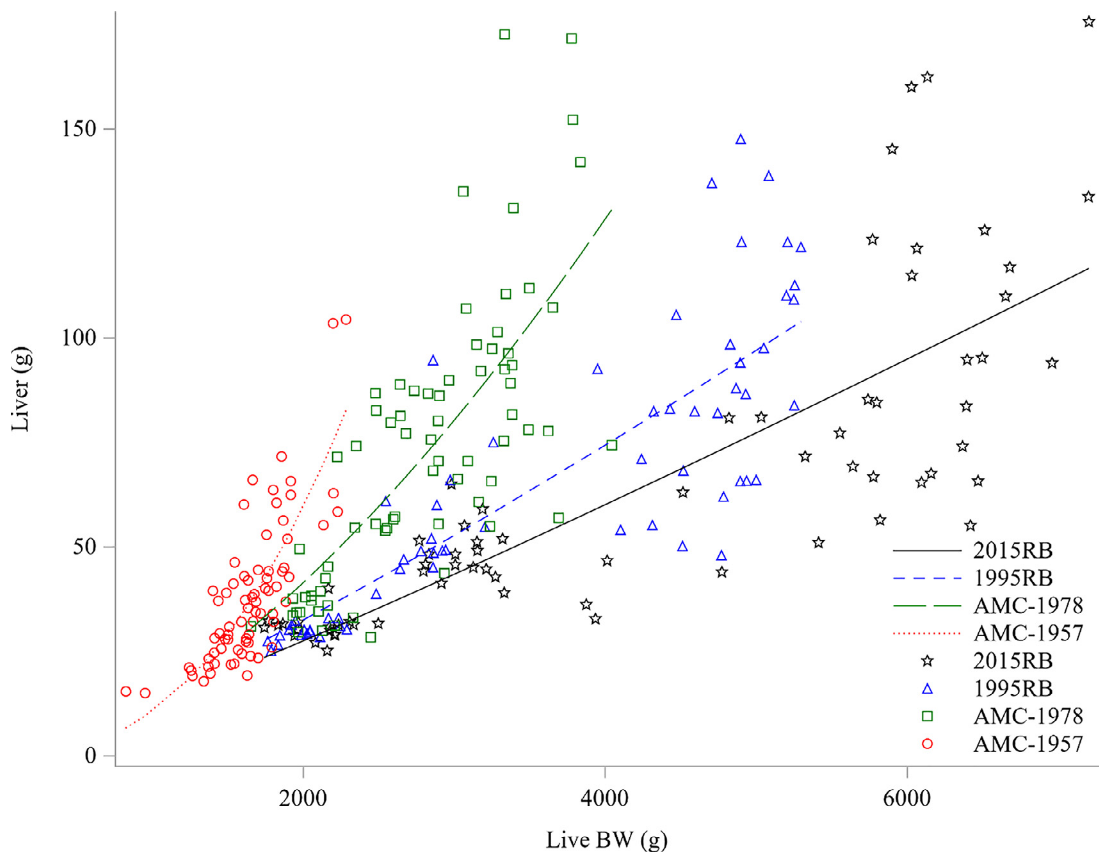


**Figure 6.** Nonlinear covariance curves for liver weight of University of Alberta Meat Control (AMC) strains unselected since 1957 and 1978, and 1995 Random Bred (1995RB) and the 2015 Random Bred (2015RB) strains originated from the University of Arkansas.

**Table 10.** BW, and carcass traits at photostimulation (22 wk) of pullets from unselected broiler strains[1] on ad libitum or restricted[2] feed intake treatments.

| Effect | Treatment (T) | Strain (S) | BW | SEM | Breast | SEM | Fatpad | SEM | Ovary | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | g | | | | | | | |
| S | | AMC-1957 | 1,548[d] | 32 | 236[d] | 6.2 | 31[c] | 2.4 | 15.2 | 3.1 |
| | | AMC-1978 | 2,577[c] | 48 | 382[c] | 9.7 | 135[b] | 7.7 | 14.1 | 3.5 |
| | | 1995RB | 3,417[b] | 42 | 577[b] | 10.5 | 189[a] | 8.9 | 9.5 | 3.1 |
| | | 2015RB | 4,039[a] | 115 | 907[a] | 27.7 | 165[ab] | 11.4 | 20.6 | 4.9 |
| T | Restricted | | 1,944[b] | 23 | 343[b] | 5.5 | 33[b] | 1.9 | 5.7[b] | 1.4 |
| | Ad lib | | 3,846[a] | 64 | 708[a] | 14.9 | 227[a] | 8.1 | 24.0[a] | 3.5 |
| S × T | Restricted | AMC-1957 | 1,546[e] | 35 | 237[f] | 5.3 | 30[d] | 3.9 | 13.7[ab] | 3.8 |
| | | AMC-1978 | 2,092[d] | 51 | 317[e] | 8.9 | 59[c] | 5.0 | 7.5[bc] | 4.0 |
| | | 1995RB | 2,009[d] | 39 | 369[d] | 10.4 | 34[d] | 3.7 | 0.8[c] | 0.1 |
| | | 2015RB | 2,130[d] | 53 | 450[c] | 16.5 | 10[e] | 2.3 | 0.7[c] | 0.1 |
| | Ad lib | AMC-1957 | 1,549[e] | 53 | 234[f] | 11.2 | 32[d] | 2.8 | 16.7[ab] | 4.9 |
| | | AMC-1978 | 3,061[c] | 82 | 447[c] | 17.2 | 212[b] | 14.6 | 20.7[ab] | 5.8 |
| | | 1995RB | 4,825[b] | 74 | 785[b] | 18.2 | 343[a] | 17.5 | 18.2[abc] | 6.2 |
| | | 2015RB | 5,949[a] | 223 | 1364[a] | 52.8 | 319[a] | 22.6 | 40.4[a] | 9.8 |
| Source of variation | | | Probability | | | | | | | |
| S | | | < 0.001 | | < 0.001 | | < 0.001 | | 0.26 | |
| T | | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | |
| S × T | | | < 0.001 | | < 0.001 | | < 0.001 | | 0.019 | |

[a-f]Means within column and within effect with no common superscript differ ($P < 0.05$).

[1]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

modern breeders, which is consistent with our findings of reduced heat production in modern strains compared to that of the AMC-1957 and AMC-1978 strains.

## Ovary Weight

At 22 wk (prior to photostimulation) there was no significant difference in ovary weight between strains, but there was considerable variation between hens within strains as evidenced by relatively large SEM values (Table 10). Some of the variation was likely related to having both feeding treatments within each of these strain means. Across all strains, pullets that had been fed ad libitum had more ovary development (24.0 g) than did restricted pullets (5.7 g) at 22 wk. The level of feed restriction used delayed the "normal" onset of ovary development seen in the ad libitum fed hens prior to photostimulation. Ovary weight at sexual maturity was lower in the AMC-1957 strain (44.9 g) than in the other strains (Table 11). The greatest ovary weight was seen in the 2015RB hens (73.6 g). These data were likely influenced by full-feeding as overall, restricted birds had lower ovary weight (50.6 g) compared to ad libitum-fed hens (64.9 g). These data suggest that the 2015RB birds had a tendency ($P = 0.062$, Table 11) to have heavier ovary weights under conditions of ad libitum feeding than the older lines, although the number of LYF was not affected by feeding treatment (Supplementary Table 1). As mature BW has increased with genetic selection, so has the weight of the ovary under such conditions. This is likely a reflection of the larger liver in the more modern strains, as the liver provides the egg yolk precursors for the ovary.

## Oviduct Weight

Oviduct weight at sexual maturity followed the same trend as did ovary weight. The three more modern lines started lay with a higher oviduct weight than did the AMC-1957 line ($P < 0.001$, Table 11). Level of feeding did not influence oviduct weight. These data suggest that there is a set point for oviduct weight that has changed over time, but that it may be resistant to level of feed intake, unlike ovary weight.

## F1 Follicle Weight

The weight of the largest ovarian follicle at sexual maturity was lower in the AMC-1957 hens (8.4 g) compared to the three other lines (11.0−12.0 g; Supplementary Table 1). Feeding level did not influence the weight of the largest follicle, but feed restriction reduced the number of LYF by 1. There were no strain differences in the number of LYF.

## Body Conformation Measurements

Ad libitum feeding resulted in wider breasts for the 1995RB and 2015RB strains but did not affect the AMC-1957, AMC-1978 strains. Over the last 60 yr, breast width has increased with genetic selection ($P < 0.001$, Table 12), which contributes to a heavier BW of the modern birds. Keel length of the 1995RB and 2015RB birds was significantly longer than the older strains regardless of feeding treatment ($P < 0.001$, Table 12). Thresholds of fat and protein mass are required leading to the onset of lay.

Among feed restricted birds, shank length was similar among all strains, which were significantly shorter than the ad libitum-fed birds except the AMC-1957, which was not affected by feeding treatment. Robinson et al. (2007) noted that feed restriction can limit shank length throughout the rearing period due to significant manipulation of the BW profile. The AMC-

**Table 11.** BW, and carcass traits at sexual maturity of pullets from unselected broiler strains[1] on ad libitum or restricted[2] feed intake treatments.

| Fate | Effect | Treatment (T) | Strain (S) | ASM[3] | SEM | BW | SEM | Breast | SEM | Fatpad | SEM | Ovary | SEM | Oviduct | SEM | F1 | SEM |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | d | | g | | | | | | | | | | number | |
| Maturity (B) | S | | AMC-1957 | 159.3$^{b}$ | 1.4 | 1,772$^{d}$ | 40 | 250$^{d}$ | 6.8 | 48$^{c}$ | 3.9 | 44.9$^{c}$ | 2.2 | 46.6$^{b}$ | 1.6 | 8.4$^{c}$ | 0.2 |
| | | | AMC-1978 | 161.6$^{b}$ | 1.5 | 2,962$^{c}$ | 49 | 425$^{c}$ | 10.8 | 156$^{b}$ | 7.2 | 57.6$^{b}$ | 2.0 | 59.3$^{a}$ | 1.7 | 11.0$^{b}$ | 0.3 |
| | | | 1995RB | 169.6$^{a}$ | 2.4 | 3,795$^{b}$ | 68 | 606$^{b}$ | 20.4 | 195$^{a}$ | 8.9 | 55.1$^{b}$ | 2.7 | 58.9$^{a}$ | 2.9 | 11.2$^{ab}$ | 0.4 |
| | | | 2015RB | 170.5$^{a}$ | 1.6 | 4,476$^{a}$ | 103 | 1049$^{a}$ | 31.8 | 159$^{b}$ | 9.3 | 73.6$^{a}$ | 4.6 | 60.2$^{a}$ | 2.1 | 12.4$^{a}$ | 0.3 |
| | T | Restricted | | 174.0$^{a}$ | 0.9 | 2,552$^{b}$ | 28 | 450$^{b}$ | 6.7 | 75$^{b}$ | 3.1 | 50.6$^{b}$ | 1.4 | 57.6 | 1.2 | 11.0 | 0.2 |
| | | Ad lib | | 156.5$^{b}$ | 1.5 | 3,951$^{a}$ | 63 | 715$^{a}$ | 18.8 | 204$^{a}$ | 7.0 | 64.9$^{a}$ | 2.7 | 55.0 | 1.8 | 10.5 | 0.3 |
| | S × T | Restricted | AMC-1957 | 157.7$^{c}$ | 1.9 | 1,732$^{f}$ | 53 | 250$^{e}$ | 8.7 | 45$^{f}$ | 4.8 | 43.5 | 2.5 | 45.6 | 2.3 | 8.1$^{d}$ | 0.3 |
| | | | AMC-1978 | 171.9$^{b}$ | 1.7 | 2,573$^{e}$ | 69 | 355$^{d}$ | 8.7 | 101$^{c}$ | 8.3 | 51.9 | 2.6 | 60.5 | 3.0 | 11.1$^{b}$ | 0.3 |
| | | | 1995RB | 180.4$^{a}$ | 2.1 | 2,866$^{d}$ | 59 | 496$^{c}$ | 11.4 | 87$^{cd}$ | 6.9 | 47.7 | 3.5 | 64.4 | 2.0 | 11.4$^{b}$ | 0.4 |
| | | | 2015RB | 186.0$^{a}$ | 1.5 | 3,037$^{d}$ | 44 | 698$^{b}$ | 20.7 | 66$^{de}$ | 4.3 | 59.4 | 2.4 | 59.8 | 2.4 | 13.3$^{a}$ | 0.3 |
| | | Ad lib | AMC-1957 | 160.9$^{c}$ | 2.1 | 1,813$^{f}$ | 61 | 251$^{e}$ | 10.4 | 52$^{ef}$ | 6.1 | 46.3 | 3.6 | 47.7 | 2.1 | 8.7$^{cd}$ | 0.3 |
| | | | AMC-1978 | 151.4$^{c}$ | 2.5 | 3,351$^{c}$ | 70 | 494$^{c}$ | 19.8 | 211$^{b}$ | 11.9 | 63.2 | 3.0 | 58.1 | 1.9 | 10.8$^{b}$ | 0.5 |
| | | | 1995RB | 158.8$^{bc}$ | 4.3 | 4,724$^{b}$ | 122 | 715$^{b}$ | 39.1 | 303$^{a}$ | 16.4 | 62.5 | 4.2 | 53.5 | 5.5 | 11.1$^{abc}$ | 0.8 |
| | | | 2015RB | 155.0$^{c}$ | 2.8 | 5,915$^{a}$ | 202 | 1401$^{a}$ | 60.1 | 252$^{ab}$ | 18.0 | 87.7 | 9.0 | 60.6 | 3.4 | 11.5$^{b}$ | 0.5 |
| Fate | Source of variation | | | Probability | | | | | | | | | | | | | |
| Maturity (B) | S | | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | |
| | T | | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | 0.23 | | 0.17 | |
| | S × T | | | < 0.001 | | < 0.001 | | < 0.001 | | < 0.001 | | 0.062 | | 0.25 | | 0.014 | |

[a-f]Means within column and within effect with no common superscript differ ($P < 0.05$)

[1]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

[3]Age at sexual maturity (defined as age at second egg).

**Table 12.** Frame size indicators of pullets from unselected broiler strains[1] on ad libitum or restricted[2] feed intake treatments.

| Fate | Effect | Treatment (T) | Strain (S) | Shank length | SEM | Keel length | SEM | Breast width | SEM |
|---|---|---|---|---|---|---|---|---|---|
| | | | | mm | | | | | |
| 22 wk (A) | S | | AMC-1957 | $97.5^{c}$ | 1.0 | $129.0^{c}$ | 1.4 | $66.9^{d}$ | 1.6 |
| | | | AMC-1978 | $105.9^{b}$ | 0.9 | $145.0^{b}$ | 1.7 | $82.3^{c}$ | 1.7 |
| | | | 1995RB | $106.3^{b}$ | 0.8 | $165.2^{a}$ | 1.4 | $95.8^{b}$ | 1.7 |
| | | | 2015RB | $110.7^{a}$ | 0.7 | $167.4^{a}$ | 2.0 | $106.8^{a}$ | 3.1 |
| | T | Restricted | | $100.8^{b}$ | 0.5 | $142.7^{b}$ | 1.1 | $74.4^{b}$ | 1.1 |
| | | Ad lib | | $109.4^{a}$ | 0.6 | $160.6^{a}$ | 1.2 | $101.5^{a}$ | 1.8 |
| | S × T | Restricted | AMC-1957 | $96.8^{d}$ | 1.1 | $129.1^{cd}$ | 2.2 | $66.7^{e}$ | 1.4 |
| | | | AMC-1978 | $103.1^{c}$ | 1.2 | $138.8^{c}$ | 2.2 | $75.3^{d}$ | 1.4 |
| | | | 1995RB | $100.3^{cd}$ | 0.8 | $151.0^{b}$ | 2.0 | $77.9^{cd}$ | 2.4 |
| | | | 2015RB | $103.0^{c}$ | 1.1 | $152.0^{b}$ | 2.2 | $77.6^{cde}$ | 3.2 |
| | | Ad lib | AMC-1957 | $98.3^{cd}$ | 1.6 | $129.0^{d}$ | 1.9 | $67.0^{de}$ | 2.8 |
| | | | AMC-1978 | $108.7^{b}$ | 1.2 | $151.3^{b}$ | 2.5 | $89.2^{c}$ | 3.1 |
| | | | 1995RB | $112.3^{b}$ | 1.3 | $179.4^{a}$ | 1.8 | $113.7^{b}$ | 2.3 |
| | | | 2015RB | $118.4^{a}$ | 0.8 | $182.8^{a}$ | 3.4 | $136.0^{a}$ | 5.2 |
| Maturity (B) | S | | AMC-1957 | $98.1^{c}$ | 0.8 | $132.3^{d}$ | 1.2 | $71.1^{d}$ | 1.5 |
| | | | AMC-1978 | $106.6^{b}$ | 0.8 | $146.2^{c}$ | 1.1 | $89.9^{c}$ | 1.1 |
| | | | 1995RB | $106.7^{b}$ | 0.6 | $164.6^{b}$ | 1.6 | $103.8^{b}$ | 2.0 |
| | | | 2015RB | $114.7^{a}$ | 0.8 | $177.0^{a}$ | 1.7 | $120.3^{a}$ | 2.8 |
| | T | Restricted | | $102.5^{b}$ | 0.5 | $148.6^{b}$ | 0.8 | $86.4^{b}$ | 1.1 |
| | | Ad lib | | $110.6^{a}$ | 0.5 | $161.4^{a}$ | 1.2 | $106.2^{a}$ | 1.6 |
| | S × T | Restricted | AMC-1957 | $98.0^{g}$ | 1.0 | $131.6^{f}$ | 1.5 | $70.9^{e}$ | 1.9 |
| | | | AMC-1978 | $103.6^{de}$ | 1.2 | $141.3^{e}$ | 1.1 | $83.9^{d}$ | 1.5 |
| | | | 1995RB | $102.0^{ef}$ | 0.8 | $157.9^{cd}$ | 2.0 | $93.5^{c}$ | 2.3 |
| | | | 2015RB | $106.3^{cd}$ | 1.0 | $163.6^{bc}$ | 1.8 | $97.4^{c}$ | 2.7 |
| | | Ad lib | AMC-1957 | $98.1^{fg}$ | 1.2 | $132.9^{f}$ | 1.9 | $71.3^{e}$ | 2.4 |
| | | | AMC-1978 | $109.6^{bc}$ | 0.9 | $151.0^{d}$ | 2.0 | $96.0^{c}$ | 1.7 |
| | | | 1995RB | $111.4^{b}$ | 0.8 | $171.4^{b}$ | 2.5 | $114.0^{b}$ | 3.3 |
| | | | 2015RB | $123.1^{a}$ | 1.1 | $190.5^{a}$ | 2.9 | $143.3^{a}$ | 4.8 |
| Fate | Source of variation | | | Probability | | | | | |
| 22 wk (A) | S | | | < 0.001 | | | | < 0.001 | |
| | T | | | < 0.001 | | | | < 0.001 | |
| | S × T | | | < 0.001 | | | | < 0.001 | |
| Maturity (B) | S | | | < 0.001 | | | | < 0.001 | |
| | T | | | < 0.001 | | | | < 0.001 | |
| | S × T | | | < 0.001 | | | | < 0.001 | |

[a-g]Means within column and within effect with no common superscript differ ($P < 0.05$).

[1]AMC-1957 and AMC-1978: University of Alberta Meat Control strains unselected since 1957 and 1978, respectively. 1995RB: 1995 Random-bred, and 2015RB: 2015 Random-bred strains originated from the University of Arkansas.

[2]Restricted birds were fed restricted amounts to achieve a modern-day target BW profile. Given that the 2015RB strain was a combination of Ross 308 and Cobb strains, the modern-day target BW profile was an average of the 2015RB target BW profile for those strains.

1957 strain had the shortest shanks of all strains ($P <$ 0.001, Table 12) regardless of feeding treatment. Although Lindholm et al. (2018) did not find any differences in bone strength of broiler breeders reared under a daily or 5/2 feeding program, the effect of feed restriction on bone strength might be investigated in future studies.

## Age at Sexual Maturity

The timing of sexual maturity varied significantly between strains, with the older genetic lines (AMC-1957 and AMC-1978) reaching sexual maturity earlier than the 1995RB and 2015RB strains (Table 11; $P < 0.001$). The difference of approximately 10 d between age at sexual maturity of the 1995RB and 2015RB strains was likely due to the degree of feed restriction of these lines. The impact of feed restriction overall was a delay in sexual maturity by 17.5 d. These data support the ovary weight data collected at 22 wk showing that ad libitum fed pullets had greater ovary development prior to photostimulation. From the interaction analyses, it can be seen that on a strain basis, feed restriction had no effect on the AMC-1957 lines (a nonsignificant delay of 3.2 d to reach sexual maturity) but affected the other strains as follows: (AMC-1978: 20.5 day delay; 95RAN: 21.6 day delay; 2015RB: 31.0 day delay). Clearly, bringing these four genetic lines to a single common BW profile caused the greatest delay in sexual maturation in the most severely feed-restricted line (i.e., 2015RB).

Many researchers have hypothesized that minimum age, BW, and body composition are required for sexual maturation to advance in broiler breeders (e.g., Katanbaf et al., 1989; Lewis et al., 2007). The extent of the effects of feed restriction on sexual maturity varied between genetic lines. Under ad libitum feeding conditions there were no strain differences in the age of sexual maturity, suggesting that age was the last threshold to be reached under ad libitum feeding conditions. However, there was a positive relationship between the degree of feed restriction and the age of sexual maturity. Frontier lines were drawn delimiting the lowest BW and the lowest age at sexual maturity (Figure 7). Minimum BW at sexual maturity increased as a result of commercial selection since 1957 in broiler breeders. However, there was not clear evidence that commercial selection for broiler traits affected the age threshold. Age at

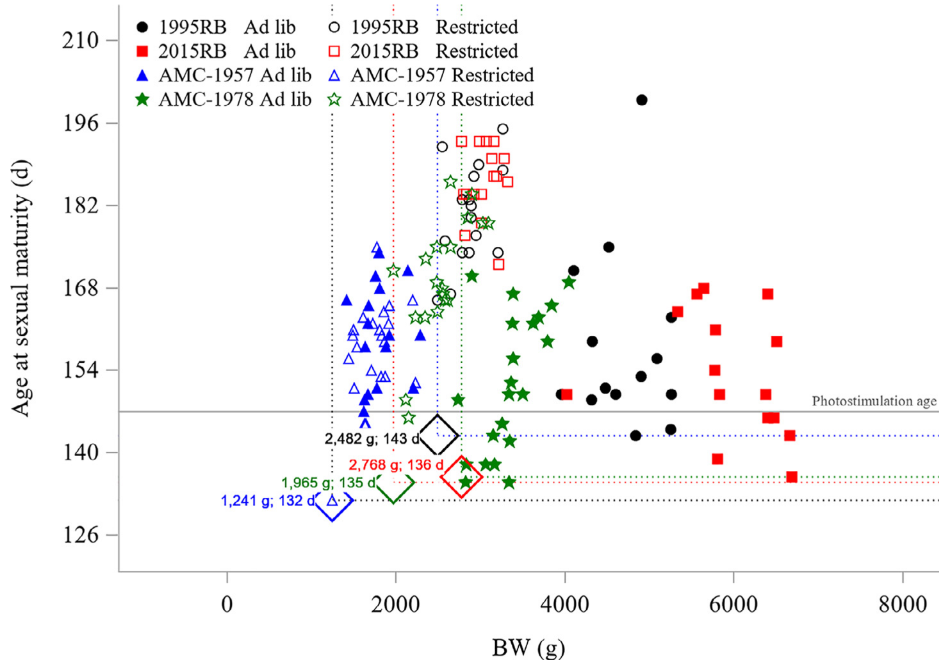


**Figure 7.** Body weight and age at sexual maturity (defined as age at second egg) of pullets from unselected broiler strains since 1957 and 1978 on ad libitum (empty shapes) or restricted (filled shapes) feeding treatments. Dotted frontier lines suggest minimum BW and age thresholds at the onset of lay in the current study.

sexual maturity in broiler breeder pullets can be advanced either by earlier photostimulation or by growing pullets at a faster rate to reach 2,100 g at 15 wk of age (Ciacciariello and Gous, 2005). Increasing prepubertal and pubertal BW gains by more than 15% of the breeder-recommended target BW triggered fat metabolism and yolk precursors synthesis in precision-fed breeders, which consequently advanced sexual maturity (Afrouziyeh et al., 2022a). As described previously, leading up to the onset of lay, breeders should not only reach a threshold BW, but should also deposit a minimum threshold amount of body fat to attain sexual maturity (Bornstein et al., 1984; Sun et al., 2006).

Genetic progress over 60 yr has resulted in a high yielding, fast growing, feed efficient broiler, which creates consequences for the modern broiler breeder. To investigate the effects of genetic selection in broiler breeders over the last decades on their reproductive fitness, the current study compared four random-bred populations. The main focus of the selection in modern breeders has been to increase growth, yield of specific meat portions, and feed efficiency; breast muscle weight increased through sexual maturity in modern breeders, which indicates that growth is a metabolic priority over reproduction in highly-selected birds. However, as fat deposition is energetically expensive, the unintended consequence has been to select for reduced body fatness in modern broiler breeders. Body fat stores are important to initiate puberty and also serve as a reservoir of energy during energetically-demanding times such as the development of an ovary, peak production, or during periods of stress. With genetic selection strategies and nutrient prioritization and increased growth potential, feed restriction programs have resulted in a level of fat stores in the modern broiler breeder hen that are marginally sufficient to support reproduction. The increased degree of feed restriction, combined with the lack of fat reserves may make the modern broiler breeder less able to handle stress or disruption in nutrients. With limited nutrients, reduced energy reserves and a drive for breast growth, the modern breeders have less body fat reserves upon which to draw when faced with the typical stress and challenges experienced by breeders under commercial conditions. Thus, potential strategies to optimize broiler breeder growth trajectory should be considered to alleviate the negative effects of severe feed restriction on broiler breeders. More research is needed to optimize broiler breeder feeding programs. The objective function for such optimization needs to consider the level of growth restriction and concomitant feed restriction level in broiler breeders without compromising animal welfare, environmental, and economic factors.

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## DISCLOSURES

The authors declare that there is no conflict of interest.

## SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.psj.2022.101957.

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