Effects of broiler genetic strain and dietary amino acid reduction on (part I) growth performance and internal organ development

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ABSTRACT Genetic selection in broilers has resulted in improved growth performance, meat yield, and feed conversion efficiency. However, consumers have become increasingly concerned about modern broiler welfare that is related to their rapid growth rate, which may be alleviated by nutrient dilution. This study was conducted to investigate the effects of dietary amino acid (**AA**) reduction on the growth performance and internal organ development of different genetic strains of broilers. A randomized completed block design with a factorial arrangement of 10 treatments (5 strains × 2 AA levels) was used. The 5 different strains of broilers were fed either a control diet, with digestible AA (lysine, total sulfur AA, and threonine) at the highest recommended levels for the 5 strains, or an AA-reduced diet, with the digestible AA being 20% lower than the control diet. Feed conversion ratio was increased by AA reduction in all 5 strains during day 0–14, 14–28, and 28–41 but was not affected from day 41–55. Body weight and feed intake responses to AA reduction varied in the different strains and ages of birds. Liver weight relative to BW on day 40, and weights of the duodenum and jejunum relative to BW on day 60 were increased by decreasing the dietary AA concentration. These results indicate that the birds had adjusted their organ growth and metabolism in response to increases in digestion, absorption, and utilization efficiency to accommodate a decrease in dietary AA content. Surprisingly, the cost of feed required to produce the same BW was decreased in 4 of 5 strains on both day 41 and 55, which was largely because of the lower price of the diets containing reduced AA levels and the later compensatory growth experienced by the birds fed AA-reduced diets. In the future, when dietary AA levels need to be adjusted to control growth rate and improve welfare status, the genetic strain, age of the birds, and targeted goals need to be taken into consideration.

Key words: amino acid, broiler, growth, internal organ, strain

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INTRODUCTION

Intensive genetic selection has improved growth rate, feed usage efficiency, breast size, and meat yield in modern broilers (Zuidhof et al., 2014). In comparison with an unselected strain from 1957, growth rate has increased 4 folds, feed conversion ratio (FCR) has been cut in half, and breast yield has increased 30–37% at 42 D of age in modern Ross 308 broilers (Zuidhof et al., 2014). However, selection has also caused unintended traits in modern broilers that are associated with rapid growth (Kokoszyński et al., 2017), including increased skeletal/leg defects (Robinson et al., 1992; Wijtten et al., 2010), metabolic disorders (Trocino et al., 2015), and meat quality defects (Cruz et al., 2017; Livingston et al., 2019). Research has shown that the incidence and severity of these problems can be alleviated by slowing growth. There are different ways to slow growth. These include feed restriction and nutrient dilution. In the present study, dietary amino acids (**AA**), including lysine (**Lys**), total sulfur AA (**TSAA**), and threonine (**Thr**), were reduced by 20% to control growth. In a companion study (unpublished), it was found that 20% AA reduction lowered the incidence of severe woody breast, a metabolic disorder in breast muscle (Kuttappan et al., 2016), at day 42 of age and lowered the incidence of moderate woody breast at day 56 of age.

Amino acids serve as both energy sources and building blocks for body tissues. The development of an ideal

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protein model, the availability of synthesized and crystalline AA, and a digestible AA concept allow maximum broiler growth performance at lower crude protein levels and associated reduced feed costs (Emmert and Baker, 1997). In addition, decreasing dietary crude protein or AA levels could decrease environmental pollution by reducing nitrogen excretion (Hernandez et al., 2012).

Methionine, Lys, and Thr are the first 3 limiting AA in corn–soybean meal–based broiler diets. Amino acid requirements are usually evaluated to achieve maximum growth performance, including BW, BW gain (**BWG**), feed intake (**FI**), **FCR** (FI/BWG), and meat yield (Sakomura et al., 2005). The estimation of AA requirements depends on the criteria being measured and the mathematical model used (Kidd et al., 1998; Leclercq, 1998). Welfare, immunity, organ development, and economic return have often been ignored in AA requirement studies (Corzo et al., 2005; Conde-Aguilera et al., 2013; Cemin et al., 2017).

Compensatory growth is rapid growth that follows a period of reduced nutrient intake upon a return to a normal diet (Rezaei and Hajati, 2010). The degree of compensatory growth can be affected by the types and levels of nutrient dilution, levels of feed restriction, lengths of feed restriction, bird age and strain, and duration of the compensatory period (Yang et al., 2015). Previous studies have shown that BW decreases and FCR increases during early protein dilution and feed restriction. However, these can be recovered by day 44 to 49 in various strains of broilers (Rezaei and Hajati, 2010; Bodle et al., 2018). Nevertheless, an excessive reduction in dietary AA may impact internal organ development and decrease meat deposition (Zhan et al., 2006).

The growth performance of broilers is closely related to internal organ development. Growth rate is partially controlled by the distribution of growth among the different organs (Lilja, 1983). Mechanical digestion occurs in the gizzard (Svihus, 2011), whereas nutrient digestion and absorption occurs mainly in the small intestine. Furthermore, duodenum weight is known to increase as BWG increases (Wijtten et al., 2010).

The liver is an organ that is integral to the growth of the organism. It is involved in multiple functions within the digestive, metabolic, immune, and reproductive systems. The liver facilitates the digestion and absorption of carbohydrates, protein, and fat (Zaefarian et al., 2019). The relative liver weights of various broiler strains have increased from 1957 to 1978 and again in 2005 (Zuidhof et al., 2014). The liver can easily adapt to changes in dietary factors (Zaefarian et al., 2019). For example, if the AA profile of a diet is not balanced, the excess AA will either be catabolized to form uric acid and excreted from the body or will be synthesized to carbohydrates and fat, with the liver being responsible for both processes (Chin and Quebbemann, 1978; Zaefarian et al., 2019). Glucose, Lys, and fat in the liver may affect FI with these effects on FI varying among strains (Denbow, 2015).

Another important factor which is often ignored when evaluating the nutrient requirements of broilers is economic return. The most profitable levels may not necessarily allow for maximum growth (Costa et al., 2001; Sterling et al., 2003; Ebling et al., 2013). Lower dietary levels of Lys and Met have been shown to decrease BW and BWG from day 1 to 47. However, feed cost per kg of BWG was decreased and gross margin return was increased by lowering the Lys and Met levels in the diets of Cobb 500 and Ross 308 broilers. In addition, even though Ross 308 broilers experienced a higher BWG, they had a higher feed cost per kg of BWG than did the Cobb 500 birds. This was mainly due to the higher FCR in the Ross 308 birds (Ebling et al., 2013). Although a higher AA density feed is more expensive, the increase in growth that it leads to makes it more cost effective. The cost of feed to produce 1 kg of BW or carcass is decreased when Met increased from 80 to 100% of the recommended level (Zhai et al., 2016).

In previous studies, the growth performance of broilers has been shown to respond differently to dietary AA changes (Sterling et al., 2006; Wijtten et al., 2010). The current study was designed to investigate the effects of a 20% AA reduction in the content of the diets of 5 modern commercial broiler strains on their intestine and internal organ development, as well as their metabolic rate, growth performance, compensatory growth, and mortality. With these factors considered together, the economic return of this dietary reduction will be determined.

MATERIALS AND METHODS

Birds

The experiment was conducted following the principles and specific guidelines of the Institutional Animal Care and Use Committee at Mississippi State University. Eggs were collected from 5 commercial broiler breeder strains of similar age (30 wk). Strains 1 and 2 have a similar genetic background, and strains 4 and 5 have a similar genetic background. Strains 1, 2, and 3 were from the same female line but are from a different male parental line. All eggs were incubated in a single-stage incubator (Chick Master, Medina, OH). The incubator was divided into 4 blocks, with each block consisting of 5 egg flats, and 90 eggs from one strain were randomly assigned to each flat. On day 11 of incubation, eggs were candled, and dead and infertile eggs were removed. On day 18 of incubation, eggs were transferred to hatching baskets and placed in a hatcher unit (Chick Master, Medina, OH). On day 21, a total of 1,280 (256 birds/strain) chicks were hatched and randomly distributed into 8 blocks in an environmentally controlled broiler house. Each block consisted of 10 pens, and there were 16 birds (straight run, including both male and female) per pen (0.0846 m^2/bird). Each pen was randomly assigned to one of the 10 treatment groups (5 genetic strains × 2 AA levels).

Diets and Management

The nutritional compositions of the corn and soybean meal used in the diets were analyzed by near-infrared spectroscopy (FOSS XDS, Denmark) before formulating the diets. Birds of each strain were fed either a control diet or an AA-reduced diet. The control diet was formulated to meet the highest recommended digestible AA (Lys, TSAA, and Thr) requirements of the 5 strains (Cobb-Vantress, 2018; Aviagen, 2019). In AA-reduced diets, the digestible AA (Lys, TSAA, and Thr) were 20% lower than the recommended levels (Table 1). The birds were fed in 4 feeding phases. These were the starter (day 0–14), grower (day 14–28), finisher (day 28–41), and withdrawal (day 41–60) grow-out period phases. Each pen was equipped with one hanging feeder and 4 nipple drinkers, and water and feed were provided on an ad libitum basis. The birds received a 24L:0D photoperiod from day 0 to 7 and a 20L: 4D photoperiod from day 8 to 60.

Growth Performance

Body weight and feed weight were recorded on day 0, 14, 28, 41, and 55 on a pen basis. Body weight gain, FI, and FCR were determined between each age period, including the overall 0- to 55-D period. Mortality was recorded daily, and the BW of birds that died was accounted for when calculating FCR.

Growth Rate Growth rate was calculated by dividing BWGby initial BW in each age interval.

$$GR_{i-j} = \frac{BW_j - BW_i}{BW_i} \times 100\%$$

where $GR_{i\text{-}j}$ = growth rate from day i (initial age) to day j (end age); BW_j = BW on day j (end age); BW_i = BW on day i (initial age).

Adjusted FI Adjusted FI was calculated by dividing FI by initial BW in each age interval.

Adjusted $FI_{i\text{-}j} = FI_{i\text{-}j}/BW_{i}$ where $FI_{i\text{-}j}$ = FI from day i (initial age) to day j (end age); BWi = BW on day i (initial age).

Cost of Feed per Unit of Body Weight Feed cost/BW on day 41 = (Starter feed price × Starter FI + Grower feed price × Grower FI + Finisher feed price × Finisher FI)/BW on day 41.

Feed cost/BW on day 55 = (Starter feed price × Starter FI + Grower feed price × Grower FI + Finisher feed price × Finisher FI + Withdrawal feed price × Withdrawal FI)/BW on day 55.

Table 1. Feed ingredients composition and nutrient contents of a control diet (Control) with digestible amino acid (lysine, total sulfur amino acid, and threonine at the highest recommended level of 5 strains) and an amino acid–reduced diet (Reduced) with these 3 digestible amino acids 20% lower than the recommended level during starter (day 0–14), grower (day 14–28), finisher (day 28–41), and withdrawal (day 41–60) feeding phases.

	Starter		Grower		Finisher		Withdrawal	
Ingredients %	Control[1]	Reduced[1]	Control	Reduced	Control	Reduced	Control	Reduced
Yellow corn	54.33	62.33	55.49	68.10	67.24	73.28	69.17	76.63
Soybean meal	38.21	31.87	36.56	25.91	24.93	20.00	23.37	17.27
Poultry grease	2.50	1.15	3.60	1.67	3.50	2.37	3.50	2.30
Dicalcium phosphate	2.21	2.22	1.97	1.99	1.76	1.76	1.65	1.66
Limestone	1.28	1.31	1.17	1.22	1.10	1.12	1.05	1.08
Salt	0.34	0.34	0.34	0.34	0.34	0.35	0.35	0.35
Choline Cl (60%)	0.07	0.11	0.06	0.13	0.09	0.12	0.09	0.13
L-Lysine HCl	0.27	0.12	0.15	0.15	0.31	0.19	0.27	0.19
DL-Methionine	0.32	0.18	0.26	0.11	0.28	0.16	0.23	0.13
Premix[2]	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
L-Threonine	0.10	0.00	0.03	0.00	0.08	0.00	0.06	0.00
Ronozyme	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Stafac[3]	0.05	0.05	0.05	0.05	0.05	0.05	0.00	0.00
Sacox[4]	0.05	0.05	0.05	0.05	0.05	0.05	0.00	0.00
Feed cost ($/ton)	264.97	240.77	261.19	231.24	245.16	225.02	237.74	217.71
Calculated composition								
Crude protein, %	23.16	20.50	22.26	18.16	18.00	15.93	17.33	14.87
Ca, %	0.96	0.96	0.87	0.87	0.78	0.78	0.74	0.74
Available P, %	0.48	0.48	0.44	0.44	0.39	0.39	0.37	0.37
ME (kcal/kg)	3,009	3,009	3,100	3,100	3,199	3,199	3,225	3,225
Digestible Lys, %	1.28	1.024	1.15	0.92	1.02	0.82	0.95	0.76
Digestible Met, %	0.67	0.50	0.60	0.41	0.57	0.42	0.51	0.38
Digestible TSAA, %	0.95	0.76	0.87	0.70	0.80	0.64	0.74	0.59
Digestible Thr, %	0.86	0.69	0.77	0.62	0.68	0.54	0.64	0.51
Choline (ppm)	1,800	1,800	1,700	1,700	1,500	1,500	1,450	1,450
Sodium, %	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16
Chloride, %	0.29	0.27	0.27	0.28	0.30	0.30	0.30	0.30

Abbreviations: ME, metabolizable energy; TSAA, total sulfur amino acid.

[1]Amino acids in the control diet were at the highest recommend levels of digestible amino acid (lysine, TSAA, and threonine); Reduced diet has digestible amino acid (lysine, TSAA, and threonine) 20% lower than the control diet.

[2]Premix provided the following per kilogram of finished diet: retinyl acetate, 2.654 µg; cholecalciferol, 110 µg; DL-α-tocopherol acetate, 9.9 mg; menadione, 0.9 mg; vitamin B12, 0.01 mg; folic acid, 0.6 µg; choline, 379 mg; D-pantothenic acid, 8.8 mg; riboflavin, 5.0 mg; niacin, 33 mg; thiamine, 1.0 mg; D-biotin, 0.1 mg; pyridoxine, 0.9 mg; ethoxyquin, 28 mg; manganese, 55 mg; zinc, 50 mg; iron, 28 mg; copper, 4 mg; iodine, 0.5 mg; selenium, 0.1 mg.

[3]Stafac provided 4.4% of virginiamycin to control enteric diseases.

[4]Sacox provided 13.2% of salinomycin sodium to prevent coccidiosis.

Table 2. Body weight, body weight gain, and growth rate of 5 strains of broilers fed a control or AA-reduced diet from day 0 to 55.

Treatment		BW (g)					BW gain (g)					Growth rate[3] (%)			
Strain	Diet	D0	D14	D28	D41	D55	D0-14	D14-28	D28-41	D41-55[1]	D0-55	D0-14	D14-28	D28-41	D41-55
Strain 1		$39.7^{b,c}$	407	1,469	2,705	3,834	367	1,062	$1,230^{b,c}$	1,128	3,794	927	261	83.8	41.8^{b}
Strain 2		$39.7^{b,c}$	411	1,431	2,665	3,852	371	1,020	$1,227^{c}$	1,187	3,812	934	248	85.8	$44.6^{a,b}$
Strain 3		41.8^{a}	451	1,568	2,898	4,183	409	1,117	$1,333^{a}$	1,285	4,142	979	248	85.3	$44.5^{a,b}$
Strain 4		39.4^{c}	416	1,448	2,748	4,041	377	1,032	$1,300^{a,b}$	1,297	4,002	957	248	90.1	47.4^{a}
Strain 5		40.2^{b}	395	1,330	2,508	3,705	355	935	$1,173^{c}$	1,197	3,665	883	236	88.9	47.9^{a}
SEM[2]		0.20	2.9	12.9	26.7	45.9	2.9	11.1	18.1	32.4	45.6	8.7	2.2	1.24	1.19
	Control	40.1	430	1,529	2,823	4,043	390	1,099	$1,291^{a}$	1,220	4,003	973	255	84.5	43.2^{b}
	Reduced	40.2	402	1,369	2,587	3,803	361	968	$1,214^{b}$	1,218	3,763	899	241	89.1	47.2^{a}
	SEM	0.13	1.8	8.2	16.9	29.0	1.8	7.0	11.6	20.5	29.1	5.5	1.4	0.783	0.75
Strain 1	Control	39.5	$419^{c,d}$	$1,508^{b,c}$	$2,764^{b,c}$	$3,884^{b,c}$	$380^{b,c,d}$	$1,089^{b,c}$	1,255	1,120	$3,844^{b,c}$	$961^{a,b}$	$260^{a,b}$	83.4^{c}	40.5
Strain 1	Reduced	39.8	395^{e}	$1,430^{c,d}$	$2,648^{c,d}$	$3,783^{c}$	355^{f}	$1,035^{c,d}$	1,204	1,136	$3,744^{c}$	892^{c}	262^{a}	84.2^{c}	43.0
Strain 2	Control	39.5	$416^{c,d}$	$1,457^{c,d}$	$2,722^{c,d}$	$3,862^{b,c}$	$377^{c,d,e}$	$1,041^{c,d}$	1,250	1,140	$3,822^{b,c}$	$953^{a,b}$	$250^{a,b,c,d}$	$85.8^{b,c}$	41.8
Strain 2	Reduced	39.9	$405^{d,e}$	$1,404^{d,e}$	$2,608^{c,d}$	$3,842^{b,c}$	$365^{d,e,f}$	$999^{d,e}$	1,204	1,233	$3,802^{b,c}$	$915^{b,c}$	$247^{b,c,d}$	$85.8^{b,c}$	47.3
Strain 3	Control	42.0	463^{a}	$1,642^{a}$	$3,007^{a}$	$4,247^{a}$	421^{a}	$1,180^{a}$	1,364	1,240	$4,205^{a}$	$1,002^{a}$	$255^{a,b,c}$	83.0^{c}	41.3
Strain 3	Reduced	41.5	439^{b}	$1,493^{b,c}$	$2,789^{b,c}$	$4,119^{a,b}$	397^{b}	$1,054^{b,c,d}$	1,303	1,330	$4,078^{a,b}$	$956^{a,b}$	$240^{c,d}$	$87.7^{a,b,c}$	47.7
Strain 4	Control	39.3	$434^{b,c}$	$1,558^{b}$	$2,913^{a,b}$	$4,229^{a}$	$395^{b,c}$	$1,123^{a,b}$	1,356	1,316	$4,190^{a}$	$1,007^{a}$	$259^{a,b}$	$87.0^{a,b,c}$	45.2
Strain 4	Reduced	39.5	397^{e}	$1,338^{e}$	$2,583^{d}$	$3,853^{b,c}$	$358^{e,f}$	941^{e}	1,244	1,278	$3,814^{b,c}$	$907^{b,c}$	237^{d}	$93.2^{a,b}$	49.7
Strain 5	Control	40.1	$418^{c,d}$	$1,480^{b,c,d}$	$2,711^{c,d}$	$3,993^{a,b,c}$	$378^{b,c,d}$	$1,061^{b,c,d}$	1,231	1,282	$3,952^{a,b,c}$	$943^{b,c}$	$254^{a,b,c}$	83.2^{c}	47.4
Strain 5	Reduced	40.3	372^{f}	$1,180^{f}$	$2,305^{e}$	$3,418^{d}$	332^{g}	808^{f}	1,114	1,113	$3,378^{d}$	823^{d}	217^{e}	94.5^{a}	48.4
SEM		0.28	4.1	18.3	37.8	64.9	4.1	15.7	25.8	45.8	64.5	12.3	3.1	1.75	1.68
P-value	Strain	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.002	<0.0001	<0.0001	<0.0001	0.003	0.004
	Diet	0.496	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.955	<0.0001	<0.0001	<0.0001	0.0001	0.0004
	Strain × Diet	0.552	0.0007	<0.0001	0.0004	0.0003	0.0007	<0.0001	0.483	0.032[1]	0.0003	0.005	<0.0001	0.014	0.499

[a–f]Means in a column not sharing a common superscript were different ($P < 0.05$).

[1]Tukey's test was not able to separate treatments means of BW gain from day 41 to 55.

[2]SEM = standard error of mean; n = 16, 40, and 8 for treatments of strain, diet, and interaction of strain and diet, respectively.

[3]Growth rate was calculated by dividing BW gain by initial BW in each period. For example, day 14–28 growth rate = day 14–28 BW gain/D 14 BW × 100%.

Gross Margin Return Gross margin return/bird = BW × whole body price* - feeding cost.

Gross margin return/kg of bird = (BW × whole body price* - feeding cost)/BW.

*The whole body price was $1.704/kg at the time of calculation on September 13, 2019 (https://search.ams.usda.gov/mnreports/PYTBROILERFRYER.pdf).

Internal Organ Sampling

On day 0, 2 birds/strain in each of the 4 blocks in the hatcher were randomly selected for sampling before bird placement (8 birds/strain). On day 8, 22, and 40, 1 bird/pen was randomly selected for sampling, and on day 60, 1 male bird/pen was selected for sampling. The birds were humanely euthanized by CO_2 asphyxiation before being dissected. Bird BW, residual yolk weight, and body temperature were measured on day 0. The BW, carcass weights, and body temperatures of the birds were measured on day 8, 22, 40, and 60. The weights of the visceral organs including the proventriculus, gizzard, liver, bursa, and all 3 parts of the small intestine were excised and measured on day 40 and 60. The lengths of the duodenum, jejunum, and ileum were measured as well.

Statistical Analysis

A randomized complete block design with a 5 (strains) × 2 (control vs. AA reduced) factorial arrangement of treatments was used in this study. Diet and strain were designated as fixed effects, and the block was designated as a random effect. A two-way ANOVA using the PROC GLM procedure of SAS, version 9.4, was used to analyze BW, BWG, growth rate relative to BW, FI, and adjusted FI, FCR, feed cost, internal organ weights, and small intestine lengths. Percentage data normality was evaluated using the PROC UNIVARIATE procedure before analysis. When significant differences were observed among treatments, Tukey–Kramer comparison test was conducted to separate treatment means. Chi-square analysis using PROC LIFETEST was used to analyze mortality data. A Wilcoxon comparison test was conducted to separate treatment means. The partial correlation analysis was applied to study the relationships of body temperature and BW and carcass weight on day 0, 14, 22, 40, and 60. Levels of significance were set at $P \leq 0.05$.

RESULTS

The results are reported in Tables 2–11. In each table from Tables 2–6 and 11, the main effect means of genetic strain and diet are followed by the interactive means of strain and diet. In Tables 7–10, only main effect means are listed because there were no significant strain and diet interactions for any of the variables tested in these tables. Because the objective of this study was to compare the responses of the various tested variables to a dietary reduction in AA within each strain, only the differences caused by a dietary AA reduction within each strain are presented in this section and later discussed. The variable means for each strain and differences among the various strains are only shown in the tables but not presented in the text of the Results section. In the tables, means and *P* values for the main effects

Table 3. Feed intake and adjusted feed intake of 5 strains of broilers fed a control or AA-reduced diet from day 0 to 55.

Treatment		Feed intake (g)					Adjusted feed intake by BW[2]			
Strain	Diet	Day 0–14	Day 14–28	Day 28–41	Day 41–55	Day0–55	Day 0–14	Day 14–28	Day 28–41	Day 41–55
Strain 1		497	1,630	2,285^{b}	2,724	7,136	12.53	4.01	1.56	1.01^{b}
Strain 2		504	1,584	2,291^{b}	2,845	7,224	12.68	3.86	1.60	1.07^{a,b}
Strain 3		525	1,694	2,402^{a}	3,024	7,644	12.57	3.76	1.54	1.05^{a,b}
Strain 4		492	1,561	2,363^{a,b}	3,011	7,427	12.50	3.76	1.64	1.10^{a}
Strain 5		475	1,432	2,153^{c}	2,745	6,804	11.80	3.63	1.64	1.10^{a}
SEM[1]		4.25	12.8	22.9	42.0	61.5	0.128	0.026	0.016	0.016
	Control	512	1,590	2,325^{a}	2,864	7,291	12.77	3.70	1.52	1.02^{b}
	Reduced	485	1,570	2,272^{b}	2,876	7,203	12.06	3.91	1.67	1.12^{a}
	SEM	2.69	8.11	14.5	26.5	38.9	0.081	0.017	0.010	0.010
Strain 1	Control	507^{a,b,c}	1,602^{b,c}	2,293	2,656^{c}	7,058^{d}	12.84^{a,b}	3.83^{c}	1.52^{d,e}	0.96
Strain 1	Reduced	487^{c,d}	1,657^{a,b}	2,278	2,793^{b,c}	7,215^{c,d}	12.22^{a,b}	4.20^{a}	1.59^{c,d}	1.06
Strain 2	Control	509^{a,b,c}	1,544^{c,d}	2,293	2,800^{b,c}	7,146^{d}	12.89^{a}	3.71^{c,d}	1.57^{c,d,e}	1.03
Strain 2	Reduced	498^{b,c,d}	1,624^{a,b,c}	2,289	2,890^{a,b,c}	7,300^{a,b,c,d}	12.47^{a,b}	4.01^{b}	1.63^{b,c}	1.11
Strain 3	Control	534^{a}	1,704^{a}	2,414	2,952^{a,b}	7,604^{a,b,c}	12.71^{a,b}	3.68^{c,d}	1.47^{e}	0.98
Strain 3	Reduced	516^{a,b}	1,684^{a,b}	2,389	3,095^{a}	7,685^{a}	12.44^{a,b}	3.84^{b,c}	1.60^{c,d}	1.12
Strain 4	Control	509^{a,b,c}	1,605^{b,c}	2,428	3,084^{a}	7,626^{a,b}	12.96^{a}	3.70^{c,d}	1.56^{c,d,e}	1.06
Strain 4	Reduced	475^{d,e}	1,516^{d}	2,298	2,939^{a,b}	7,228^{b,c,d}	12.04^{b}	3.82^{c}	1.72^{a,b}	1.14
Strain 5	Control	500^{b,c,d}	1,494^{d}	2,199	2,829^{a,b,c}	7,021^{d}	12.45^{a,b}	3.57^{d}	1.49^{e}	1.05
Strain 5	Reduced	450^{e}	1,370^{e}	2,106	2,661^{c}	6,587^{e}	11.15^{c}	3.68^{c,d}	1.79^{a}	1.16
SEM		6.01	18.1	32.4	59.3	87.0	0.181	0.037	0.023	0.023
P-value	Strain	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0006
	Diet	<0.0001	0.093	0.012	0.762	0.114	<0.0001	<0.0001	<0.0001	<0.0001
	Strain × Diet	0.018	<0.0001	0.227	0.014	0.0004	0.046	0.002	<0.0001	0.755

$^{a–e}$Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]SEM = standard error of mean; n = 16, 40, and 8 for treatments of strain, diet, and interaction of strain and diet, respectively.
[2]Adjusted feed intake (FI) by BW = FI (g)/initial BW (g) × 100%. For example, FI by BW 14–28 = day 14–28 FI/D 14 BW × 100%.

Table 4. Feed conversion ratio (from day 0 to 55) and feed cost to produce 1 kg BW (on day 41 and 55) of 5 strains of broilers fed a control or AA-reduced diet.

Treatment		Feed conversion ratio							Feed cost/BW ($/kg)[2]		Gross margin return ($/bird)		Gross margin return ($/kg BW)	
Strain	Diet	Day 0-14	Day 14-28	Day 28-41	Day 41-55	Day 0-28	Day 0-41	Day 0-55	Day 41	Day 55	Day 41	Day 55	Day 41	Day 55
Strain 1		1.348[a]	1.532	1.870[a,b]	2.337	1.482	1.654	1.796	0.393	0.440	3.481	4.755	1.286	1.240
Strain 2		1.353[a]	1.547	1.884[a]	2.327	1.493	1.668	1.818	0.396	0.442	3.421	4.766	1.283	1.237
Strain 3		1.281[c]	1.514	1.833[a,b]	2.300	1.447	1.620	1.762	0.385	0.431	3.752	5.223	1.294	1.248
Strain 4		1.304[b,c]	1.512	1.824[b]	2.283	1.453	1.624	1.774	0.387	0.434	3.550	5.034	1.292	1.245
Strain 5		1.334[a,b]	1.544	1.844[a,b]	2.151	1.481	1.652	1.769	0.391	0.434	3.232	4.617	1.288	1.245
SEM[1]		0.0082	0.0066	0.0153	0.0325	0.0055	0.0078	0.0090	0.0017	0.0028	0.0375	0.0649	0.0017	0.0027
	Control	1.309[b]	1.444	1.823[b]	2.271	1.407	1.593	1.740	0.397	0.446	3.621	4.988	1.282	1.233
	Reduced	1.339[a]	1.616	1.879[a]	2.288	1.536	1.694	1.828	0.384	0.426	3.353	4.770	1.296	1.253
	SEM	0.0052	0.0042	0.0097	0.0206	0.0034	0.0049	0.0057	0.0011	0.0018	0.0236	0.0410	0.0010	0.0017
Strain 1	Control	1.331	1.469[c]	1.845	2.279[a,b]	1.432[d]	1.615[d]	1.751[b,c,d]	0.404[a,b]	0.450[a,b]	3.526[b,c,d]	4.777[c,d]	1.276[e,f]	1.229[d,e]
Strain 1	Reduced	1.364	1.595[b]	1.894	2.394[a]	1.533[b,c]	1.694[a,b]	1.842[a]	0.383[d,e,f]	0.429[c,d,e]	3.434[c,d]	4.733[d]	1.296[a,b,c]	1.250[a,b,c]
Strain 2	Control	1.348	1.478[c]	1.854	2.377[a]	1.442[d]	1.624[c,d]	1.793[a,b,c]	0.405[a]	0.458[a]	3.471[c,d]	4.720[d]	1.275[f]	1.221[e]
Strain 2	Reduced	1.358	1.617[b]	1.914	2.277[a,b]	1.544[b]	1.711[a,b]	1.843[a]	0.388[c,d,e,f]	0.427[d,e]	3.370[d]	4.813[b,c,d]	1.292[a,b,c,d]	1.252[a,b]
Strain 3	Control	1.265	1.441[c,d]	1.812	2.312[a]	1.392[e]	1.574[d]	1.724[d,e]	0.393[b,c,d]	0.444[a,b,c,d]	3.872[a]	5.253[a]	1.287[c,d,e]	1.236[b,c,d,e]
Strain 3	Reduced	1.297	1.586[b]	1.854	2.288[a,b]	1.503[c]	1.667[b,c]	1.800[a,b,c]	0.377[f]	0.419[e]	3.632[a,b,c]	5.193[a,b,c]	1.302[a]	1.260[a]
Strain 4	Control	1.283	1.426[d]	1.810	2.314[a]	1.392[e]	1.578[d]	1.740[c,d,e]	0.395[a,b,c]	0.446[a,b,c]	3.744[a,b]	5.221[a,b]	1.285[d,e,f]	1.234[c,d,e]
Strain 4	Reduced	1.324	1.598[b]	1.838	2.252[a,b]	1.519[b,c]	1.670[b,c]	1.809[a,b]	0.380[e,f]	0.422[e]	3.355[d]	4.847[a,b,c,d]	1.299[a,b]	1.257[a]
Strain 5	Control	1.317	1.405[d]	1.792	2.073[b]	1.381[e]	1.575[d]	1.691[e]	0.392[c,d]	0.435[b,c,d,e]	3.491[c,d]	4.972[a,b,c,d]	1.287[c,d]	1.244[a,b,c,d]
Strain 5	Reduced	1.351	1.683[a]	1.896	2.229[a,b]	1.582[a]	1.730[a]	1.848[a]	0.391[c,d,e]	0.433[b,c,d,e]	2.972[e]	4.263[e]	1.289[b,c,d]	1.246[a,b,c,d]
SEM		0.0116	0.0093	0.0216	0.0460	0.0077	0.0110	0.0128	0.0024	0.0040	0.0529	0.0917	0.0024	0.0039
P-value	Strain	<0.0001	0.0002	0.036	0.0009	<0.0001	0.0001	0.0002	0.0002	0.035	<0.0001	<0.0001	0.0002	0.035
	Diet	0.0001	<0.0001	0.0001	0.561	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0004	<0.0001	<0.0001
	Strain × Diet	0.725	<0.0001	0.485	0.026	<0.0001	0.007	0.001	0.003	0.004	0.0003	0.0003	0.0031	0.0081

[a–f]Means in a column not sharing a common superscript were different ($P < 0.05$).

Feed cost/BW on day 55 was calculated by (Feed price day 0–14 × FI day 0–14 + Feed price day 14–28 × FI day 14–28 + Feed price day 28–41 × FI day 28–41 + Feed price day 41–55 × FI day 41–55)/BW on day 55.

The prices for the diets are listed in Table 1.

Abbreviation: FI = feed intake.

[1]SEM = standard error of mean; n = 16, 40, and 8 for treatments of strain, diet, and interaction of strain and diet, respectively.

[2]Feed cost/BW on day 41 was calculated by (Feed price day 0–14 × FI day 0–14 + Feed price day 14–28 × FI day 14–28 + Feed price day 28–41 × FI day 28–41)/BW on day 41.

Table 5. The carcass and internal organ weights (g) of 5 strains of broilers fed a control or AA-reduced diet on day 40.

Strain	Diet	Carcass[1]	Proventriculus	Gizzard	Heart	Liver	Pancreas	Bursa	Spleen
Strain1		2,120	8.02	37.14^{a}	11.54^{a,b,c}	45.26^{a,b}	4.54	3.09^{b}	2.33
Strain2		2,032	7.42	33.58^{a,b}	11.21^{b,c}	42.60^{b}	4.32	2.99^{b}	2.03
Strain3		2,260	8.27	35.11^{a}	13.05^{a}	48.81^{a}	4.69	3.94^{a}	2.05
Strain4		2,138	8.19	34.51^{a}	12.32^{a,b}	46.68^{a,b}	4.67	3.73^{a,b}	1.96
Strain5		1,967	6.84	29.95^{b}	10.63^{c}	42.49^{b}	4.24	3.60^{a,b}	2.09
SEM[2]		43.8	0.293	1.014	0.418	1.410	0.179	0.210	0.147
	Control	2,176	7.78	35.98^{a}	11.84	45.14	4.68^{a}	3.60	2.13
	Reduced	2,031	7.71	32.14^{b}	11.66	45.19	4.30^{b}	3.34	2.05
	SEM	27.7	0.185	0.641	0.264	0.892	0.113	0.133	0.093
Strain 1	Control	2,128^{a,b}	8.69^{a}	39.19	11.32	45.06	4.70	3.42	2.48
Strain 1	Reduced	2,113^{a,b}	7.34^{a,b}	35.09	11.76	45.47	4.38	2.76	2.18
Strain 2	Control	2,124^{a,b}	7.51^{a,b}	36.52	11.98	43.67	4.57	2.89	1.80
Strain 2	Reduced	1,940^{a,b}	7.33^{a,b}	30.65	10.43	41.53	4.06	3.10	2.27
Strain 3	Control	2,278^{a}	8.13^{a,b}	35.34	12.84	49.82	4.85	4.04	2.07
Strain 3	Reduced	2,242^{a}	8.41^{a,b}	34.88	13.27	47.80	4.54	3.84	2.03
Strain 4	Control	2,173^{a,b}	7.58^{a,b}	35.52	11.94	43.71	4.60	3.91	2.12
Strain 4	Reduced	2,104^{a,b}	8.80^{a}	33.50	12.70	49.66	4.75	3.54	1.80
Strain 5	Control	2,179^{a,b}	6.99^{a,b}	33.32	11.13	43.46	4.70	3.75	2.20
Strain 5	Reduced	1,755^{c}	6.68^{b}	26.58	10.13	41.52	3.78	3.45	1.99
SEM		61.9	0.414	1.434	0.591	1.994	0.253	0.298	0.208
P-value	Strain	0.0002	0.003	0.0002	0.0001	0.011	0.262	0.011	0.477
	Diet	0.0004	0.792	<0.0001	0.627	0.967	0.021	0.171	0.551
	Strain × Diet	0.010	0.036	0.268	0.168	0.145	0.305	0.705	0.318

[a–c]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]Carcass weight = chicken BW without the proventriculus, gizzard, heart, liver, pancreas, bursa of Fabricius, spleen, or intestine.
[2]SEM = standard error of mean; n = 16, 40, and 8 for treatments of strain, diet, and interaction of strain and diet, respectively.

of strain, diet, and their interactions are provided in that order for each variable. When a significant diet × strain interaction occurred for a particular variable, only those strains in which a significant response to AA treatment was observed were noted in the Results section. Those strains in which there was no significant response to AA treatment were not included.

Growth Performance

Mortality Bird mortality was not affected by any treatment (P = 0.983). Overall mortality was low (ranged from 0.781 to 3.125%), indicating that the birds were exposed to a normal grow-out environment.

Body Weight On day 14, strains 1, 3, 4, and 5 that were fed AA-reduced diets exhibited lower BW than birds

Table 6. The relative weight (%) of carcass and internal organs to BW of 5 strains of broilers fed a control or AA-reduced diet on day 40.

Strain	Diet	Carcass[1]	Proventriculus	Gizzard	Heart	Liver	Pancreas	Bursa	Spleen
Strain1		85.34^{b}	0.324	1.50	0.464	1.83	0.185	0.128	0.090^{a,b}
Strain2		86.44^{a,b}	0.301	1.43	0.477	1.82	0.184	0.136	0.083^{a,b}
Strain3		86.29^{a,b}	0.305	1.35	0.513	1.82	0.176	0.156	0.074^{b}
Strain4		85.76^{a,b}	0.329	1.39	0.491	1.87	0.189	0.152	0.075^{b}
Strain5		86.89^{a}	0.306	1.34	0.473	1.86	0.188	0.154	0.093^{a}
SEM[2]		0.342	0.0108	0.039	0.0146	0.045	0.0069	0.0079	0.0045
	Control	86.63^{a}	0.309	1.44^{a}	0.471	1.78^{b}	0.186	0.145	0.080
	Reduced	85.66^{b}	0.317	1.36^{b}	0.496	1.90^{a}	0.183	0.146	0.085
	SEM	0.216	0.0068	0.025	0.0092	0.028	0.0044	0.0050	0.0028
Strain 1	Control	85.92	0.354^{a}	1.59	0.457	1.82	0.194	0.136	0.094
Strain 1	Reduced	84.76	0.295^{a,b}	1.41	0.472	1.83	0.176	0.120	0.087
Strain 2	Control	86.66	0.308^{a,b}	1.49	0.488	1.79	0.187	0.118	0.073
Strain 2	Reduced	86.21	0.294^{a,b}	1.37	0.465	1.85	0.181	0.154	0.093
Strain 3	Control	86.61	0.301^{a,b}	1.36	0.494	1.80	0.177	0.163	0.070
Strain 3	Reduced	85.97	0.309^{a,b}	1.34	0.532	1.84	0.176	0.149	0.078
Strain 4	Control	86.39	0.301^{a,b}	1.42	0.473	1.74	0.184	0.157	0.077
Strain 4	Reduced	85.13	0.358^{a}	1.36	0.510	2.00	0.193	0.147	0.072
Strain 5	Control	87.57	0.283^{b}	1.34	0.444	1.75	0.188	0.148	0.089
Strain 5	Reduced	86.20	0.330^{a,b}	1.33	0.502	1.97	0.189	0.160	0.098
SEM		0.483	0.0152	0.055	0.0205	0.063	0.0097	0.0112	0.0063
P-value	Strain	0.034	0.157	0.057	0.201	0.854	0.699	0.097	0.008
	Diet	0.002	0.427	0.027	0.058	0.006	0.611	0.826	0.223
	Strain × Diet	0.768	0.003	0.521	0.375	0.278	0.718	0.134	0.190

[a, b]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]Carcass weight = chicken BW without the proventriculus, gizzard, heart, liver, pancreas, bursa of Fabricius, spleen, or intestine.
[2]SEM = standard error of mean; n = 16, 40, and 8 for treatments of strain, diet, and combination of strain and diet, respectively.

Table 7. The small intestine weight, length, relative weight to BW, and ratio of weight to length of 5 strains of broilers fed a control or AA-reduced diet on day 40.

		Weight (g)			Relative weight to BW (%)			Length (cm)			Ratio of weight to length (g/cm)		
Strain	Diet	Duo[2]	Jej[2]	Ile[2,3]	Duo	Jej	Ile	Duo	Jej	Ile	Duo	Jej	Ile
Strain1		12.07	22.67[a,b,c]	18.95	0.477	0.913	0.766	28.86	69.22	72.50	0.418	0.327[a,b]	0.262
Strain2		11.85	20.58[b,c]	16.57	0.505	0.875	0.706	27.88	67.06	70.54	0.431	0.307[b]	0.240
Strain3		11.92	23.40[a,b]	18.67	0.457	0.897	0.719	28.88	69.72	71.88	0.405	0.336[a,b]	0.261
Strain4		12.07	23.89[a]	18.72	0.470	0.962	0.752	28.81	69.76	69.93	0.418	0.358[a]	0.265
Strain5		10.35	20.10[c]	16.37	0.463	0.899	0.727	27.03	63.45	66.89	0.387	0.323[a,b]	0.249
SEM[1]		0.462	0.809	0.690	0.0164	0.0317	0.0279	0.855	1.882	2.119	0.0129	0.0104	0.0089
	Control	11.96	22.64	18.42	0.469	0.904	0.736	28.51	68.54	72.18[a]	0.417	0.332	0.260
	Reduced	11.34	21.62	17.30	0.479	0.915	0.732	28.07	67.15	68.51[b]	0.407	0.329	0.250
	SEM	0.292	0.512	0.435	0.0103	0.0201	0.0176	0.543	1.190	1.340	0.0082	0.0066	0.0056
P-value	Strain	0.059	0.003	0.012	0.325	0.359	0.497	0.436	0.103	0.267	0.272	0.019	0.243
	Diet	0.139	0.162	0.074	0.502	0.704	0.885	0.567	0.415	0.046	0.388	0.744	0.218
	Strain × Diet[4]	0.322	0.466	0.084	0.484	0.506	0.232	0.397	0.644	0.579	0.130	0.239	0.061

[a–c]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]SEM = standard error of mean; n = 16 and 40 for treatments of strain and diet, respectively.
[2]Abbreviations: Duo = duodenum; Jej = jejunum; Ile = ileum.
[3]Tukey test was not able to separate means of strain effects on ileum weights.
[4]When the results of interaction were not significantly different, the data of means were not shown in the table.

that were fed the control diet ($P = 0.0007$) (Table 2). On day 28 and 41, strains 3, 4, and 5 that were fed AA-reduced diets exhibited a lower BW than those fed a control diet ($P < 0.0001$ and $P = 0.0004$). On day 55, only strains 4 and 5 that were fed the AA-reduced diet exhibited a lower BW than those fed the control diet ($P = 0.0003$).

Body Weight Gain During day 0–14, an AA reduction in the diet lowered BWG in strains 1, 3, 4, and 5 ($P = 0.0007$), and during day 14–28, an AA reduction in the diet lowered BWG in strains 3, 4, and 5 ($P < 0.0001$). Furthermore, during day 28–41, an AA reduction in the diet lowered BWG across all strains ($P < 0.0001$). From day 0 to 55, only strains 4 and 5 fed an AA reduced diet exhibited a lower BWGwhen compared with those fed the control diet ($P = 0.0003$).

Growth Rate Growth rate was calculated by dividing BWG by initial BW in each period. During day 0–14, strains 1, 4, and 5 which were fed AA-reduced diets exhibited a lower GR than those same strains fed the control diet ($P = 0.005$). During day 14–28, an AA reduction in the diet lowered GR in strains 4 and 5 ($P < 0.0001$). However, during day 28–41, strain 5 birds that were fed the AA-reduced diet exhibited a higher GR than those fed the control diet ($P = 0.014$). During day 41–55, birds that were fed the AA-reduced diet exhibited a higher GR than did the broilers fed the control diet ($P = 0.0004$).

Feed Intake Strains 4 and 5 that were fed AA-reduced diets exhibited a lower FI than did broilers fed the control diet during the day 0–14 ($P = 0.018$) and 14–28 ($P < 0.0001$) intervals (Table 3). During day 28–41, an AA reduction in the diet lowered FI for all strains ($P = 0.012$). Overall, from day 0 to 55, AA reduction in the diet lowered FI only in strain 5 ($P = 0.0004$).

Feed Intake Adjusted for BW Adjusted FI was calculated by dividing FI by initial BW in each period. Similar to absolute FI, an AA reduction in the diet also lowered adjusted FI in strains 4 and 5 in the day 0–14 interval. However, FI relative to BW was increased in strains 1 and 2 during day 14–28 ($P = 0.002$) and increased in strains 3, 4, and 5 during day 28–41 ($P < 0.0001$)

Table 8. The carcass and internal organ weights (g) of 5 strains of broilers fed a control or AA-reduced diet on day 60.

Strain	Diet	Carcass[1]	Proventriculus	Gizzard	Heart	Liver	Pancreas	Bursa	Spleen
Strain1		3,964[b]	10.96	47.65	21.61[a,b]	70.48	5.78[b]	3.26	4.70
Strain2		4,174[a,b]	11.78	51.20	21.81[a,b]	68.65	6.76[a,b]	4.12	5.36
Strain3		4,480[a]	11.66	50.33	21.11[b]	71.18	6.04[a,b]	4.59	4.59
Strain4		4,565[a]	11.81	50.64	24.16[a]	75.96	7.09[a]	4.51	5.35
Strain5		3,993[b]	11.09	45.74	20.14[b]	69.04	6.17[a,b]	4.36	5.58
SEM[2]		107	0.496	1.493	0.716	2.506	0.271	0.342	0.385
	Control	4,353[a]	11.51	50.14	22.25	70.78	6.61	4.20	5.18
	Reduced	4,117[b]	11.41	48.09	21.28	71.34	6.13	4.14	5.05
	SEM	67.8	0.313	0.944	0.453	1.585	0.171	0.216	0.244
P-value	Strain	0.0002	0.622	0.059	0.003	0.227	0.006	0.062	0.285
	Diet	0.018	0.830	0.134	0.140	0.808	0.054	0.842	0.720
	Strain × Diet[3]	0.328	0.537	0.083	0.898	0.695	0.213	0.268	0.756

[a, b]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]Carcass weight = chicken BW without the proventriculus, gizzard, heart, liver, pancreas, bursa of Fabricius, spleen, or intestine.
[2]SEM = standard error of mean; n = 16 and 40 for treatments of strain and diet, respectively.
[3]When the results of interaction were not significantly different, the data of means were not shown in the table.

Table 9. The relative weight (%) of carcass and internal organs to BW of 5 strains of broilers fed a control or AA-reduced diet on day 60.

Strain	Diet	Carcass[1]	Proventriculus	Gizzard	Heart	Liver	Pancreas	Bursa	Spleen
Strain1		91.27	0.256	1.07	0.461[a,b]	1.63	0.135	0.080	0.101
Strain2		91.68	0.261	1.10	0.482[a]	1.51	0.146	0.089	0.113
Strain3		91.70	0.244	1.03	0.435[b]	1.47	0.124	0.089	0.095
Strain4		91.59	0.245	1.02	0.485[a]	1.53	0.139	0.091	0.110
Strain5		91.17	0.255	1.05	0.463[a,b]	1.58	0.141	0.096	0.118
SEM[2]		0.299	0.0128	0.032	0.0115	0.047	0.0059	0.0072	0.0068
	Control	91.69	0.248	1.04	0.460	1.50	0.140	0.088	0.108
	Reduced	91.27	0.256	1.07	0.471	1.59	0.135	0.091	0.107
	SEM	0.189	0.0081	0.021	0.0073	0.030	0.0038	0.0045	0.0043
P-value	Strain	0.630	0.861	0.463	0.022	0.152	0.136	0.674	0.149
	Diet	0.126	0.482	0.238	0.313	0.054	0.362	0.673	0.934
	Strain × Diet[3]	0.312	0.255	0.261	0.424	0.399	0.448	0.785	0.608

[a, b]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]Carcass weight = chicken BW without the proventriculus, gizzard, heart, liver, pancreas, bursa of Fabricius, spleen, or intestine.
[2]SEM = standard error of mean; n = 16 and 40 for treatments of strain and diet, respectively.
[3]When the results of interaction were not significantly different, the data of means were not shown in the table.

when the birds were fed an AA-reduced diet. Moreover, independent of strain, an AA reduction in the diet increased FI adjusted to BW during day 41–55 ($P < 0.0001$).

Feed Conversion Ratio Broilers fed AA-reduced diets exhibited a greater FCR than did birds fed the control diet during day 0–14 (main effect of diet; $P = 0.0001$), 14–28 (within each strain; $P < 0.0001$), 28–41 (main effect of diet; $P = 0.0001$), 0–28 (within each strain; $P < 0.0001$), 0–41 (within each strain; $P = 0.007$), and 0–55 (with the exception of strain 2; $P = 0.001$) (Table 4). However, FCR was not affected by a dietary AA reduction from day 41–55 within each strain ($P > 0.05$).

Feed Cost and Gross Margin Return Feed cost to produce 1 kg of BW was decreased by a dietary AA reduction on day 41 ($P = 0.003$) and 55 ($P = 0.004$) in all strains except for strain 5. Accordingly, the gross margin return to produce the same amount of BW was increased by AA reduction on day 41 and 55 in all strains with the exception of strain 5 ($P = 0.003$ and 0.008). The gross margin return to grow 1 bird was decreased in strains 4 and 5 on day 41 and decreased in strain 5 on day 55 ($P = 0.0003$ and 0.0003).

Internal Organ Development

A dietary AA reduction also decreased the absolute weights of the gizzards and pancreases ($P < 0.0001$ and $P = 0.021$) and the carcass weights of strain 5 broilers ($P = 0.010$) (Table 5). A dietary AA reduction decreased the relative weights of the carcasses ($P = 0.002$) and gizzards ($P = 0.027$) of the broilers, which indicated that the absolute weights of the carcass and gizzard decreased more than BW in response to the dietary AA reduction (Table 6). However, liver weight relative to BW increased by an AA reduction ($P = 0.006$), and the relative weights of all other internal organs were not affected by the dietary AA reduction within each strain ($P > 0.05$). On day 40, the dietary AA reduction shortened ileum length ($P = 0.046$) (Table 7).

Table 10. The small intestine weight, length, relative weight to BW, and ratio of weight to length of 5 strains of broilers fed a control or AA-reduced diet on day 60.

		Weight (g)			Relative weight to BW (%)			Length (cm)			Ratio of weight to length (g/cm)		
Strain	Diet	Duo[2]	Jej[2]	Ile[2]	Duo	Jej	Ile	Duo	Jej	Ile	Duo	Jej	Ile
Strain1		16.52	29.35	22.33	0.371[a,b]	0.676[a,b]	0.498	32.20	70.59[b]	77.09[a,b]	0.512	0.415	0.292
Strain2		16.69	31.28	24.25	0.368[a,b]	0.687[a,b]	0.536	32.24	73.49[a,b]	78.71[a,b]	0.525	0.424	0.309
Strain3		15.72	30.60	22.69	0.324[b]	0.624[b]	0.470	30.31	71.09[b]	81.05[a,b]	0.518	0.430	0.274
Strain4		18.06	33.98	23.81	0.362[a,b]	0.688[a,b]	0.481	32.56	79.63[a]	84.13[a]	0.554	0.427	0.283
Strain5		17.04	32.34	23.27	0.396[a]	0.773[a]	0.537	32.22	72.54[b]	76.40[b]	0.516	0.442	0.300
SEM[1]		0.598	1.132	0.867	0.0136	0.0232	0.0198	0.774	1.762	1.843	0.0151	0.0124	0.0107
	Control	16.65	30.24	22.85	0.351[b]	0.664[b]	0.487	31.36	73.00	78.06	0.525	0.420	0.291
	Reduced	16.96	32.08	23.69	0.378[a]	0.714[a]	0.521	32.46	73.94	80.89	0.525	0.435	0.292
	SEM	0.378	0.716	0.548	0.0086	0.0147	0.0125	0.489	1.115	1.166	0.0096	0.0078	0.0068
P-value	Strain	0.095	0.060	0.532	0.011	0.003	0.057	0.273	0.003	0.024	0.290	0.695	0.189
	Diet	0.571	0.077	0.283	0.030	0.021	0.060	0.123	0.555	0.094	0.967	0.178	0.911
	Strain × Diet[3]	0.100	0.863	0.482	0.363	0.537	0.841	0.259	0.119	0.133	0.846	0.937	0.822

[a, b]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]SEM = standard error of mean; n = 16 and 40 for treatments of strain and diet, respectively.
[2]Abbreviations: Duo = duodenum, Jej = jejunum, and Ile = ileum.
[3]When the results of interaction were not significantly different, the data of means were not shown in the table.

Table 11. Body weight, carcass weight, and cloacal body temperature of 5 strains of broilers fed a control or AA-reduced diet on day 0, 8, 22, 40, and 60.

		Day 0			Day 8			Day 22			Day 40[5]		Day 60[5]	
Strain	Diet	BW (g)	YFBW[1]/BW (%)	Temp[2] (°C)	BW (g)	Carcass[3] (g)	Temp (°C)	BW (g)	Carcass (g)	Temp (°C)	BW (kg)	Temp (°C)	BW (kg)	Temp (°C)
Strain1		38.8	89.76	39.42	175^{b}	125^{b}	41.60	886^{b}	732	41.27	2.48	41.46	4.34^{b}	41.26
Strain2		41.0	90.28	39.24	173^{b}	$125^{a,b}$	41.51	932^{b}	770	41.33	2.35	41.46	$4.55^{a,b}$	41.34
Strain3		41.9	89.25	39.12	194^{a}	140^{a}	41.76	$1{,}062^{a}$	873	41.31	2.62	41.41	4.88^{a}	41.37
Strain4		39.5	89.26	39.63	172^{b}	$125^{a,b}$	41.41	$962^{a,b}$	797	41.31	2.49	41.49	4.98^{a}	41.32
Strain5		40.6	90.23	39.42	$184^{a,b}$	$135^{a,b}$	41.48	893^{b}	738	41.28	2.26	41.35	4.38^{b}	41.30
SEM[4]		1.19	0.606	0.135	4.7	3.8	0.096	21.4	18.4	0.051	0.048	0.067	0.109	0.061
	Control				186^{a}	136^{a}	41.62	982^{a}	811	41.25	2.51	41.45	4.74^{a}	41.27
	Reduced				173^{b}	125^{b}	41.48	912^{b}	753	41.35	2.37	41.42	4.51^{b}	41.37
	SEM				3.0	2.4	0.061	13.5	11.7	0.032	0.031	0.042	0.069	0.039
Strain 1	Control				182	128	41.8	932	$772^{a,b,c,d}$	41.24	2.47^{a}	41.41	4.26	41.17
Strain 1	Reduced				168	122	41.4	840	$692^{c,d}$	41.31	2.49^{a}	41.51	4.42	41.35
Strain 2	Control				175	128	41.7	959	$794^{a,b,c,d}$	41.27	2.45^{a}	41.47	4.61	41.41
Strain 2	Reduced				171	123	41.3	906	$747^{b,c,d}$	41.40	2.25^{b}	41.44	4.49	41.28
Strain 3	Control				203	148	41.8	1,067	872^{a}	41.17	2.63^{a}	41.47	5.05	41.25
Strain 3	Reduced				186	133	41.7	1,058	874^{a}	41.44	2.61^{a}	41.35	4.71	41.49
Strain 4	Control				180	132	41.4	989	$819^{a,b}$	41.33	2.51^{a}	41.47	5.18	41.24
Strain 4	Reduced				163	119	41.4	935	$776^{a,b,c,d}$	41.28	2.47^{a}	41.51	4.79	41.41
Strain 5	Control				192	142	41.5	965	$799^{a,b,c}$	41.24	2.49^{a}	41.43	4.61	41.29
Strain 5	Reduced				175	129	41.5	822	677^{d}	41.31	2.03^{c}	41.26	4.14	41.30
SEM					6.6	5.3	0.136	30.2	26.1	0.072	0.068	0.095	0.154	0.087
P-value	Strain	0.656	0.685	0.186	0.008	0.013	0.105	<0.0001	<0.0001	0.926	<0.0001	0.597	<0.0001	0.785
	Diet				0.002	0.003	0.109	0.0001	0.0002	0.060	0.002	0.567	0.021	0.091
	Strain × Diet				0.877	0.831	0.343	0.057	0.045	0.229	0.007	0.595	0.265	0.216

[a-d]Means in a column not sharing a common superscript were different ($P < 0.05$).
[1]Abbreviation: YFBW = yolk-free body weight.
[2]Temp was the abbreviation of temperature and measured in the cloaca of broilers.
[3]Carcass weight was BW without internal organs including the proventriculus, gizzard, heart, liver, pancreas, bursa, spleen, and intestine.
[4]SEM = standard error of mean; n = 16, 40, and 8 for treatments of strain, diet, and interaction of strain, respectively, and diet for day 8, 22, 40, and 60. N = 4 for day 0.
[5]Carcass weight for day 40 and 60 are listed in Tables 7 and 9.

The absolute and relative weights of the internal organs and the small intestine length data on day 60 are shown in Tables 8–10. Because there was no significant strain by diet interactions for any of the variables, only main effect means are shown. The dietary AA reduction decreased the absolute carcass weights of the birds across strains ($P = 0.018$) (Table 8).

Dietary AA reduction tended to increase the relative liver weight on day 60 ($P = 0.054$) (Table 9). The absolute weights of the jejunum were not significantly affected by strain or diet ($P > 0.05$) (Table 10). Dietary AA reduction increased relative duodenum ($P = 0.030$) and jejunum ($P = 0.021$) weights and tended to increase relative ileum weights ($P = 0.060$) across strains (Table 10).

Relationship Between Body Temperature and BW and Carcass Weight

A dietary AA reduction lowered BW on day 8 ($P = 0.002$), 22 ($P = 0.0001$), and 60 ($P = 0.021$) and lowered absolute carcass weights on day 8 ($P = 0.003$) (Table 11). Furthermore, on day 40, an AA reduction in the diet lowered the BW of birds in strains 2 and 5 ($P = 0.007$). However, cloacal body temperature was not affected by diet or strain at any age ($P > 0.05$). Nevertheless, partial correlation analysis of cloacal body temperature with whole body and carcass weights indicated that cloacal body temperature was positively correlated to BW ($P = 0.0006$) and carcass weight ($P = 0.003$) on day 60 (Table 12).

DISCUSSION

The objective of this study was to investigate the different responses of various broiler strains to a dietary AA reduction. Therefore, the discussion has focused on the birds' responses to a dietary AA reduction within strain and not across strains.

Body Weight and BWG

The BW, BWG,and FI of the various strains were affected by an AA reduction in their diets. However, the different strains responded in different ways and to different degrees. The different responses in BW among the different strains are likely related to their different genetic backgrounds. Similar genetic backgrounds are shared between strains 1 and 2 and between strains 4 and 5. Strains with similar genetic backgrounds shared common nutritional requirements and responded similarly to a dietary AA reduction. A dietary AA reduction decreased the BW of strains 4 and 5 more than it did in strains 1 and 2, which suggests that strains 4 and 5 were either more sensitive to an AA reduction or their AA requirements were higher than that of strains 1 and 2.

Lysine, Met, and Thr are the first 3 limiting AA for broilers fed a corn–soybean meal diet. Leclercq (1998) reported that dietary Lys levels were related to the body composition and growth rate of broilers. Lowering the essential AA levels of diets could lower broiler BW. Ebling et al. (2013) reported that a reduction in essential AA (Lys, TSAA, Thr, Arg, Val, and Ile) led to a decrease in the BW of Ross 308 and Cobb 500 broilers during 1–42 D of age period. Corzo et al. (2005) also found that an essential AA reduction decreased the BW of broilers belong to 3 different strains (1 high-yield strain and 2 multipurpose strains) from 14 to 56 D of age. Kheiri and Alibeyghi (2017) determined that diets with 20% higher levels of Lys and Thr than those recommended by National Research Council (1994), allowed for increases in the whole body and carcass weights of Ross 308 broilers between 21 and 42 D of age. However, Conde-Aguilera et al. (2013) reported that lowering dietary TSAA by 22% and Met by 34% (from day 7 to 42) did not affect the BW of Ross PM3 broilers at 42 D of age. Ebling et al. (2013) also reported that decreasing dietary AA levels from high to normal levels did not decrease broiler BW between 11 and 20 D of age. The inconsistency of these results may be because of physiological variances of the broiler strains used in these previous studies.

A reduction in dietary AA tended ($P = 0.078$) to cause strain 2 birds to eat more between day 14 and 28, which resulted in similar BW and BWG results between birds that were fed the control and AA-reduced diets. In contrast, the AA reduction caused strains 4 and 5 to eat less during day 0–14 and 14–28, which resulted in a lower BW and lower BWG in birds fed AA-reduced diets. It appears that strain 2 birds adjusted their FI to meet their nutrient requirements, whereas strains 4 and 5 could not make the same adjustment.

Compensatory Growth

Growth Rate and Adjusted Feed Intake Across dietary treatment, growth rate (BWG/initial BW) decreased in strains 1, 4, and 5 between 0–14 and in strains 4 and 5 between 14 and 28 of age. However, across dietary treatment, growth rate increased in strain 5 between 28 and 41 D and increased in all strains between 41 and 55 D of age. Adjusted FI/BW followed a similar trend to growth rate, in that across dietary treatment, adjusted FI decreased in strains 4 and 5 between day 0 and 14 but increased in strains 1 and 2 between day 14 and 28, strains 4, 5, and 6 between day 28 and 41, and in all strains between day 41 and 55. The transition from a decrease to an increase in adjusted FI

Table 12. Partial correlations of broiler cloacal body temperature with body and carcass weight on day 0, 8, 22, 40, and 60 of age.

	Body weight		Carcass weight	
Age	Coefficients	P-value	Coefficients	P-value
Day 0	0.1202	0.6139	-	-
Day 8	0.0313	0.8091	-0.0007	0.9958
Day 22	0.1862	0.1441	0.1901	0.1355
Day 40	0.1496	0.2418	0.1732	0.1747
Day 60	0.4429	0.0006	0.4636	0.0003

n = 160 for day 0; and 80 for day 8, 22, 40 and 60 of age.

occurred earlier in strains 1 and 2 than in strains 3, 4, and 5, which may explain why the BW and BWG were affected less by an AA reduction in strains 1 and 2 than in strains 3, 4, and 5.

Compensatory growth (also known as accelerated growth) is a phenomenon that occurs after nutrient dilution or feed restriction and is observed in birds exhibiting a higher FI relative to BW and higher growth rate relative to BW when a normal feeding program is resumed (Zubair and Leeson, 1996).

Broilers that were fed a nutritionally diluted diet (diet diluted with 25–55% rice hulls) from day 4 to 11 experienced a decrease in BW on day 11, but their BW and FCR were fully recovered by day 42 when the normal diet was fed after day 11 (Leeson et al., 1991). The birds adjusted their FI to accommodate the lower nutrient density (Leeson et al., 1991). Furthermore, in that study, it was mentioned that the birds grew fast, but their strains were not revealed. The growth rate (BWG/initial BW) of the birds was not calculated in that study (Leeson et al., 1991). Other studies indicated that broilers increased FI to compensate for a dietary AA deficiency in diets in which protein content was diluted from day 15 to 42 (Yang et al., 2015) and when AA were reduced in the diets from day 1 to 10 of age (Ebling et al., 2013). Feeding a Lys-deficient diet (95% of NRC recommendation) to Avian 34 × Avian broilers from day 1 to 18 lowered BW. Supplementation of high-Lys diets (125% of NRC-recommended levels) in the grower and finisher diets could partially compensate BW loss (Kidd et al., 1998). However, the effects of an AA reduction on FI are not consistent among previous studies. Ebling et al. (2013) found that broilers fed diets with low or normal AA levels exhibited a higher FI than when fed diets with high AA levels between 1 and 10 D of age. The birds fed diets with low or normal AA levels also did not experience differences in FI after D 10. However, Cemin et al. (2017) reported that increasing Lys from 0.77 to 1.17% in the diets of Cobb × Cobb 500 broilers caused their FI exhibit a quadratic response from day 12 to 28, with no difference occurring from 1 to 12 D of age. The differences in the results among the aforementioned studies may be because of differences in their feed/nutrient restrictions that were applied to the birds and to differences in the strains and ages of the birds used.

The main difference between this and other compensatory studies was that the AA levels in the reduction diet was low throughout the trial, but in other studies, a normal nutrition or feeding program was resumed after a short period of time. However, the birds in this study still exhibited a higher adjusted FI and experienced an increased growth rate sooner or later in all strains, even when fed 20% AA reduction diets, which suggested strong compensatory growth.

Liver Weight Leeson and Zubair (1997) conducted a study in which birds were subjected to feed restriction (50% of full fed) from 6 to 12 D of age, and were full fed from 12 to 21 D of age. Nevertheless, their BWG recovered fully by 12 to 21 D of age and their FCR had even declined between 12 and 21 of age. In the same study, Leeson and Zubair (1997) reported that the imposed feed restriction lowered absolute liver weight on day 21, but that liver weight relative to BW had increased on day 21. Similar results occurred in the present study in which an AA reduction in the diet increased relative liver weight on day 40 ($P = 0.006$) and exhibited a trend to increase relative liver weight on day 60 ($P = 0.054$). The liver is a multipurpose organ that produces bile and metabolizes carbohydrates, protein, and fat (Zaefarian et al., 2019). The increased relative weight of the liver in broilers fed the AA-reduced diet may be related to unbalanced AA profiles in the AA-reduced diet. The 20% reduction in essential AA (Lys, TSAA, and Thr) may have decreased protein synthesis and nonessential AA utilization, and the extra unused nonessential AA might have been transformed into ketoacids and ammonia in the liver. Thus, metabolic reactions in the liver might have been increased owing to the loss of nutrients and an imbalance in the AA profile. A review article has also concluded that internal organ development, especially that associated with the digestive system, adapts to increased digestion and absorption efficiency after nutrient loss (Zubair and Leeson, 1996).

Gizzard Dietary AA reduction led to a more rapid decrease in absolute gizzard weights than BW, as reflected by lower relative gizzard weights to BW on day 40. The function of the gizzard is to grind feed, with well-developed gizzards being necessary to improve nutritional utilization (Svihus, 2011). However, in modern broiler production, the gizzard has become a more nonessential organ because the grain has already been grounded in the feed mill. When birds are lacking AA in their diet, the nutrient supply to nonessential organs may decrease before their decrease to essential organs.

Intestine Dietary AA reduction led to lower carcass weights in the birds on day 60 but did not affect their internal organ weights. However, the AA reduction did increase the relative duodenum and jejunum weights of the birds. Similarly, Susbilla et al. (1994) found that a reduction in the intake of AA by 50%, through feed restriction, increased relative intestinal weight of 12 D of age. The duodenum is the main site for intestinal digestion, and the jejunum is responsible for further digestion and absorption. Therefore, an increase in the relative duodenum and jejunum weights may help support the compensatory growth of broilers before slaughter.

Amino Acid Reduction on Feed Cost and Gross Margin Return Faster growth or an improvement in feed efficiency does not always translate to higher profits. In the present study, a dietary AA reduction led to a decrease in BW and BWG and an increase in FCR in some broiler strains. The cost of feed to produce 1 kg of BW was decreased with a reduction in dietary AA in 4 of the 5 strains on both day 41 and 55, which resulted in increased gross margin returns to produce the same amount of BW in these 4 strains. The decrease in feed cost/BW is mainly due to the lower price of the AA reduced diets and the compensatory growth response in the birds fed the AA-reduced diet. To achieve a more profitable level of production, diet formulation strategies may need to be reconsidered. The most common feed formulation algorithm is least feed cost. However, maximum profit strategies will include consideration of product value. Moreover, other costs in broiler production should also be included in addition to feed cost to evaluate actual benefits. In addition, welfare issues, especially issues as a consequence of rapid growth, should be considered before adjusting feed formulas.

Feed Conversion Ratio

As expected for all strains, the AA reduction in the broiler diets increased FCR during day 0–14, 14–28, and 28–41. However, during day 14–28, FCR increased at different rates among the different strains. The FCR for strains 4 and 5 was increased more than the rest of the strains during day 14–28. The FCR results in response to AA levels in broiler diets in previous studies (Corzo et al., 2005; Dozier et al., 2007; Ebling et al., 2013) have been inconsistent. Dozier et al. (2007) reported that decreasing dietary AA density levels increased the FCR of broilers. Because Lys, Met, and Thr are directly related to muscle protein synthesis, the decrease in dietary AA decreases their BWG (Leclercq, 1998; Ebling et al., 2013). When the levels of dietary essential AA are inadequate, broilers are unable to use the diet efficiently because they cannot synthesize essential AA in the body.

The imposed AA reduction in the diets in this study affected FCR more than it did for BW and BWG. This is because some strains adjusted FI to accommodate the loss of nutrients in their diets. Nevertheless, their FCR was not affected during the last stage of grow out from day 41 to 55. This lack of effect may be owing to AA having less of an effect on the growth in the older birds as compared with that on the younger birds.

Effects of Age

The BW, BWG, FI, adjusted FI, and growth rate responses of the broilers to AA reduction varied with age. The negative effects of the AA reduction on BW decreased with bird age. The BW of 4 strains on day 14, 3 strains on day 28 and 41, and only 1 strain on day 55 were affected by the AA reduction. Broilers are less sensitive to an AA reduction with an increase in age. Dozier et al. (2007) reported that decreasing dietary AA density (Lys and TSAA from 0.98 and 0.83% to 0.88 and 0.75%) did not influence the BW or BWG of Ross 708 male broilers during day 42–56. Cemin et al. (2017) reported that the Lys requirement of Cobb 500 broilers achieving an optimal BWG was 1.20, 1.01 and 0.96% for the starter, grower, and finisher phases, respectively. Total sulfur AA, Lys, and Thr requirement decrease with age (Emmert and Baker, 1997). However, the BW and maintenance energy requirements increased as age increased (Sakomura et al., 2005). The energy level in a diet is more important than its protein content after 42 D of age (Cobb-Vantress, 2018; Aviagen, 2019), because the energy requirement increases whereas the protein requirement decreases as birds age.

Relationships of Temperature With Body and Carcass Weight

Although the reduction in dietary AA affected BW, bird body temperature was not affected by the AA reduction at any age. Partial correlation analysis showed that the body and carcass weights were not related to body temperature on day 0, 8, 22, or 40. However, higher body and carcass weights were positively associated with a higher body temperature on day 60. When birds are small, their relative body surface area is larger, so they can better regulate their body temperature. However, on day 60, when the birds became very large, they were not able to liberate heat quickly enough, even though the house temperature was only 14.4°C–16.7°C (58.0°F–62.1°F). An earlier study has reported that the relative number of capillaries and blood vessels per unit of body surface area becomes lower with rapid myofiber growth in breast muscle (Joiner et al., 2014), which may compromise the cooling capability of large birds. An insufficient cooling capability in big birds is a common problem in modern broiler production.

CONCLUSION

The effects of a reduced dietary AA concentration on BW and BWG varied among the different strains of broilers in this study. However, the AA reduction increased broiler FCR similarly among the different strains. Broiler internal organ development adjusted for the increase in nutrient digestion and absorption, to allow for the compensation of reduced AA dietary levels when birds were fed an AA-reduced diet. The negative effects of AA reduction on growth performance decreased with aging and lowering dietary AA levels decreased the total cost of feed to produce the same amount of BW, which indicates that a better performance (including faster growth, higher BW, and lower FCR) does not always equate to higher profits. In the future, when feed formulas are manipulated to control growth rate and improve welfare status, consideration should be given to genetic strain and age of the birds, as well as the targeted goals.

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