Effects of different dietary starch sources on growth and glucose metabolism of geese

C. Xu,* Z. Yang,†,1 Z. F. Yang,* X. X. He,* C. Y. Zhang,* H. M. Yang,* S. P. Rose,‡ and Z. Y. Wang*

*College of Animal Science and Technology, Yangzhou University, Yangzhou, 225009, China; †Joint International Research Laboratory of Agriculture and Agri-Product Safety of Ministry of Education of China, Yangzhou University, Yangzhou, 225009, China; and ‡The National Institute of Poultry Husbandry, Harper Adams University, Newport, UK

ABSTRACT This experiment investigated the effects of different dietary starch sources on the growth and glucose metabolism of geese. A total of 240 healthy 35-day-old male geese were selected and randomly divided into 4 groups, with 6 replicates per group and 10 geese per replicate. Four types of diets were prepared, with glutinous rice (rapidly-digestible starch), corn, indica rice and high amylose as their starch sources, and fed for 28 d. Results showed that after consuming different feeds, the blood glucose of geese first increased and then decreased, reaching its maximum value 0.5 h after feeding, and there were significant differences between the groups ($P < 0.05$). The body weight of the corn and indica rice group geese at 63 d was higher than that of the high amylose group ($P < 0.05$). The serum total cholesterol (**TCHO**) content in the glutinous rice and corn groups was higher than in the high amylose group ($P < 0.05$). The serum insulin content in the glutinous rice group was lower than in the corn and high amylose groups ($P < 0.05$), while the glucagon content was higher ($P < 0.05$). The α-amylase activities of the pancreas, jejunal chyme, and jejunal mucosa in the glutinous rice group were higher than in the indica rice and high amylose groups ($P < 0.05$). The liver glycogen content in the glutinous rice group was higher than the other groups ($P < 0.05$). The liver glucose-6-phosphate dehydrogenase (**G-6-PD**) content in the glutinous rice group was higher than the high amylose group's ($P < 0.05$), but the glycogen synthase kinase-3 β (**GSK-3β**) content was lower ($P < 0.05$). In conclusion, the corn and indica rice diets had a positive effect on the growth performance of the geese, while the high amylose diet had a negative effect. The glutinous rice diet leads to rapid release of glucose, strengthening glucose metabolism pathways such as glycogen synthesis and the pentose phosphate pathway, and further influencing lipid metabolism.

Key words: geese, starch, growth performance, glucose metabolism

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INTRODUCTION

Starch is the main carbohydrate component of cereal grain, and the most important energy source for poultry (Svihus, 2014). Its digestion and absorption plays an essential role in animal growth. Starches can be classified as amylose or amylopectin based on their chemical structure. Starches can also be categorized into rapidly digestible (**RDS**), slowly digestible (**SDS**), and resistant starches (**RS**), based on the time required for their digestion (Englyst et al., 1992). Studies have shown that high amylose starches include a high RS content (Yang et al., 2006), and the higher the amylopectin content, the more rapidly digestible the starch (Martens et al., 2018). Different cereals contain starches of different structures and digestibility (Menoyo et al., 2011; Li et al., 2017).

Differences in starch digestibility can have an impact on animals' growth performance. Gutierrez et al. (2009) concluded that differences in starch digestibility affected the growth performance of broilers. Wurding et al. (2003a) showed that increasing the dietary content of slowly digestible starch significantly increased broilers' weight gain. Doti et al. (2014) discovered, through feeding growing pigs dietary starch sources based on barley, millet, corn, and peas, that the pigs fed pea diets (high in slowly digestible starch) grew most rapidly.

Since poultry lack salivary amylase, their digestion of starch is almost entirely dependent on pancreatic

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[1]Corresponding author: zhiyang@zyu.edu.cn

α-amylase (Moran, 1982). Starch in feed is converted into glucose by amylase and disaccharidase, which is absorbed via the intestinal wall, then circulates through the blood to various organs providing energy. Glucose is also involved in glycolysis, the pentose phosphate pathway, tricarboxylic acid cycle, and other cyclic metabolic pathways (Li et al., 2019).

Glucose metabolism is central to the metabolism of all physiological substances. The rate at which starch releases glucose in the intestine affects various pathways of glucose metabolism, with further effects on protein and lipid metabolism (Li et al., 2019; Yin et al., 2019). This experiment was thus designed to study the effects of diets formulated with different starch sources on the growth performance and glucose metabolism of geese.

MATERIALS AND METHODS

Experimental Design and Diets

This animal study was approved by the Institutional Animal Care and Use Committee (**IACUC**) of the Yangzhou University Animal Experiments Ethics Committee under permit number SYXK (Su) IACUC 2021-0027. All experimental procedures involving geese were performed in accordance with the *Regulations for the Administration of Affairs Concerning Experimental Animals* approved by the State Council of the People's Republic of China. The geese in the test were all healthy, and were raised in Gaoyou Modern Agricultural Farm, Yangzhou, China.

This study used Jiangnan White Geese, a 3-line-crossed commercial Chinese white goose of intermediate size, which exhibits rapid early growth, good-quality meat, and strong tolerance and adaptability to coarse feed. A total of 240 thirty-five-day-old, healthy male geese of similar body weight (**BW**) were randomly divided into 4 experimental groups (the glutinous rice, corn, indica rice, and high amylose groups) with 6 replicates per group and 10 geese per replicate. Four experimental diets were separately prepared, using glutinous rice (high amylopectin content, almost no amylose), indica rice (relatively high amylose content), corn and high amylose as their starch sources (Table 1). The experiment was ended when the geese were 63 days old; all geese had access to feed and water ad libitum throughout the trial. The geese were reared indoors under similar environmental conditions (temperature: 26.0°C ± 3.0°C; relative humidity (**RH**): 65.5 ± 5.0%; lighting period: 16 h/day; space allocation: 0.5 m^2/goose).

Table 1. Composition and nutrient levels of geese diets (dry basis).

Items	Groups			
	A	B	C	D
Ingredients (%)				
Corn	-	57.60	-	49.40
Indica rice	-	-	53.75	-
Glutinous rice	51.00	-	-	-
Amylose	-	-	-	6.00
Soybean meal	23.20	24.20	23.45	25.00
Rice husk	9.60	9.50	10.10	9.30
Bran	12.45	4.90	9.05	6.40
Stone powder	1.10	1.10	0.90	1.20
Calcium hydrogen	1.20	1.10	1.30	1.10
Salt	0.30	0.30	0.30	0.30
Lysine	-	0.10	-	0.10
DL- methionine	0.15	0.20	0.15	0.20
Premix[1]	1.00	1.00	1.00	1.00
Total	100.00	100.00	100.00	100.00
Nutritional level[2]				
ME (MJ/kg)	10.86	10.82	10.80	10.80
Crude protein (%)	15.93	16.18	16.01	16.14
Crude fiber (%)	6.86	6.87	6.83	6.80
Lysine (%)	0.91	0.91	0.90	0.92
Methionine (%)	0.41	0.43	0.42	0.43
Total phosphorus (%)	0.61	0.59	0.60	0.61
Calcium (%)	0.85	0.82	0.83	0.86
Total starch (%)	37.92	38.84	39.77	38.16
Amylose: Amylopectin ratio	0.021	0.340	0.456	0.568

[1]One kilogram of premix contained Vitamin A, 9,000,000 IU; Vitamin D, 300,000 IU; Vitamin E, 1,800 IU; Vitamin K, 150 mg; Vitamin B1, 90 mg; Vitamin B2, 800 mg; Vitamin B6, 320 mg; Vitamin B12, 1.2 mg; nicotinic acid, 4.5 g; pantothenic acid, 1,100 mg; folic acid, 65 mg; biotin, 5 mg; Fe (as ferrous sulfate), 6 g; Cu (as copper sulfate), 1 g; Mn (as manganese sulfate), 9.5 g; Zn (as zinc sulfate), 9 g; I (as potassium iodide), 50 mg; Se (as sodium selenite), 30 mg.

[2]Crude protein, Calcium, total phosphorus and total starch are measured values; the rest are calculated values. Group A, glutinous rice diet; group B, corn diet; group C, indica rice diet; group D, high amylose diet.

Continuous Blood Glucose Monitoring

At the age of 59 d, one goose of close to average weight was selected from each replicate and placed in a stainless steel metabolic cage for feeding. The four day experimental period comprised a 3-d period of acclimation and feeding training (feeding every 2 h, 10 min per feeding) followed by one day of blood glucose determination (monitoring blood glucose changes). Blood glucose concentration measurements were performed 60 min before feeding (after 8 hours' fasting), and 15, 30, 60, 120, 180, 240, 300, and 360 min after feeding. Three blood glucose measurement tools were used: a blood collection pen, test paper, and blood glucose meter. First the blood collection needle was used to obtain a drop of blood from the leg vein of a goose. Next, a (one-time use) test strip was inserted into the blood glucose meter and the test strip blood collection port lightly touched to the blood drop. Finally, the results displayed on the glucose meter were read and recorded. All of these operations were repeated at the designated blood collection times. The blood glucose meter was provided by Simcere Zaikang Jiangsu Pharmaceutical Co., Ltd. (Nanjing, China).

Sample Collection and Index Determination

The body weight of the geese in each pen, and their feed intake, were measured using electronic scales (Rongcheng, ACS-30, Zhejiang, China) at 35 d and 63 d of age. Average daily feed intake (**ADFI**), average daily gain (**ADG**) and feed/gain (**F/G**) were calculated during this period. At 63 d of age, one goose of near-average weight was selected from each replicate for slaughter. Slaughter was carried out 0.5 h after feeding. This was because we had discovered, by continuous blood glucose monitoring, that differences in the blood glucose concentrations in experimental groups were largest, and blood glucose had basically attained its maximum value, at 0.5 h after feeding. Slaughter was performed in the laboratory' slaughter facility. After 2 min of bleeding from the neck, the bodies were quickly dissected, and samples of intestinal chyme, intestinal mucosa, pancreas, and liver were collected and cryopreserved at −80°C.

Nutrient Content of Diets

The starch assay kit was purchased from Nanjing Jiancheng Biological Engineering Institute (Nanjing, China) and used in strict accordance with its operation manual. Crude protein was determined using a FOSS Kjeltec 8400 automatic Kjeldahl nitrogen tester.

The diet samples were charred in a high temperature electric furnace until smokeless and then transferred to a muffle furnace and ashed at 550 ± 20°C for 12 h to obtain ash. The calcium content was determined by EDTA titration method. The phosphorus content was determined by molybdenum yellow colorimetric method.

Clinical Blood Parameters

At 0.5 h after the geese were fed, blood drawn from wing veins was centrifuged for 10 min at 4,500 r/min to obtain serum for measurement of biochemical indices. This was stored at −20°C prior to analysis. Serum concentrations of triglycerides (**TG**), total cholesterol (**TCHO**), total protein (**TP**), uric acid (**UA**), high-density lipoprotein (**HDL**), lactic acid (**LA**), and low-density lipoprotein (**LDL**) were measured using an automatic biochemical analyzer (UniCel DxC 800 Synchron, Beckman Coulter, CA).

Serum insulin and glucagon levels were determined using detection kits purchased from Nanjing Jiancheng Bioengineering Institute (Nanjing, China), used strictly in accordance with their operating manual.

Pancreatic and Intestinal α-Amylase Activity

After slaughter and dissection of the test goose, its intestine was removed, the contents of its jejunum quickly squeezed out, put into a freezing tube, frozen in liquid nitrogen, and placed in storage at −80°C. The jejunal intestinal contents were rinsed using 0.9% NaCl solution. Mucosal samples were scraped off using sterile glass slides, put into freezing tubes, frozen in liquid nitrogen, and placed in storage at −80°C. For pancreatic tissue sampling the same method was used. For α-amylase activity detection, kits purchased from Nanjing Jiancheng Bioengineering Institute were used in strict accordance with their operating manual.

Liver Glycogen Content

Liver samples were collected, put into freezing tubes, frozen in liquid nitrogen, and placed in storage at −80° C. Glycogen assay kits purchased from Nanjing Jiancheng Bioengineering Institute were used in strict accordance with their operating manual.

Liver Glucose Metabolism-Related Enzymes

Detection kits for glucose 6-phosphate dehydrogenase (**G-6-PD**) activity purchased from Suzhou Keming Biotechnology Co., Ltd. (Suzhou, China) were used. Glucose-6 phosphatase (**G-6-P**) and glycogen synthase kinase-3β (**GSK-3β**) contents were determined using ELISA kits purchased from Shanghai Yubo Biotechnology Co., Ltd. (Shanghai, China), in strict accordance with their operating manual.

Statistical Analysis

The experimental data were initially collated using Excel 2020, then analyzed using SPSS 20.0 software (Ver. 20.0 for Windows, SPSS, Inc., Chicago, IL). In the continuous blood glucose monitoring test, a randomized block ANOVA analysis for repeated measures, with a 4 × 9 factorial structure, was performed to investigate the effects of the 4 dietary treatment factors (starch sources) at 9 time points, and any interactions. Tukey's test was applied to indicate significant differences between treatments ($P < 0.05$). The results of the data analysis are presented as mean and standard error.

RESULTS

Changes in Blood Glucose

Figure 1 shows the changes over time of blood glucose concentrations in the geese after feeding with different sources of dietary starch. As shown in Figure 1, for all groups blood glucose concentration first increased after feeding, gradually stabilized, and finally decreased. The fastest increase in blood glucose was in the glutinous rice group, followed by the indica rice group, the corn group and high amylose corn starch group. The results in Table 2 show significant differences in blood glucose concentration ($P < 0.05$) at different times after feeding, with the highest blood glucose concentration at 0.5 h after feeding. The results in Table 3 show that the greatest differences in blood glucose concentration between the four groups occurred at 0.5 h after feeding ($P < 0.05$).

Growth Performance

Table 4 shows the effects of different sources of dietary starch on the growth of the geese from 35 to 63 d. These results indicate that different sources of dietary starch significantly affected the body weight of the geese at 63 d and their average daily gain. The 63-d body weight of

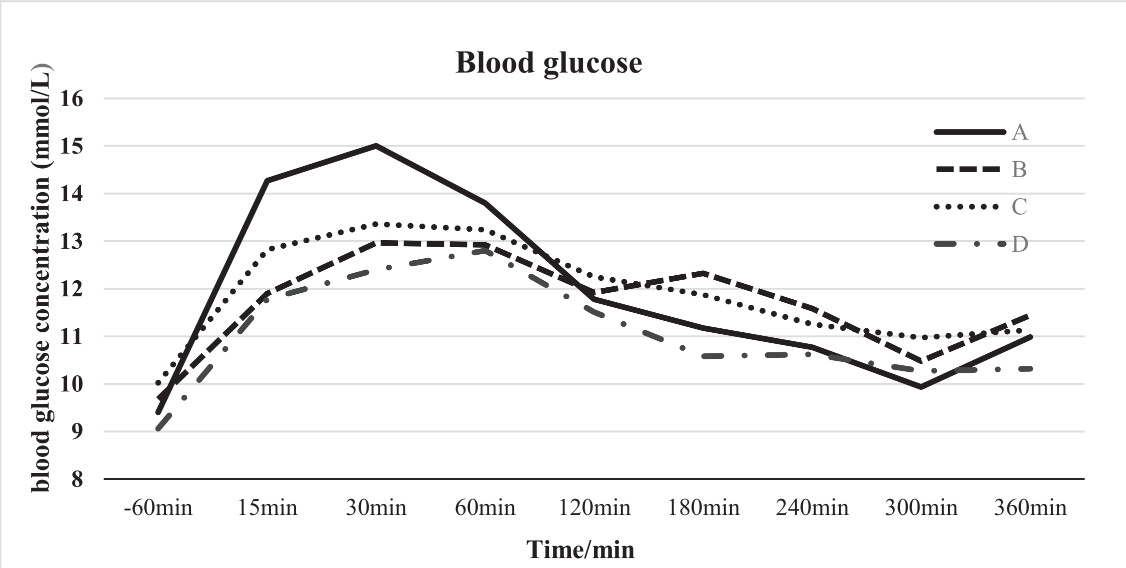

Figure 1. Blood glucose of geese fed different dietary starch sources[1]. [1]Each value represents the mean of 6 replicate pens. Group A, glutinous rice diet; group B, corn diet; group C, indica rice diet; group D, high amylose diet.

the corn and indica rice groups was significantly higher than that of the high amylose group ($P < 0.05$).

Serum Biochemical Parameters

Table 5 shows the effects of different sources of dietary starch on the serum biochemical indexes of the 63-day-old geese. These results indicate that the blood glucose of the glutinous rice group was significantly higher than that of the other groups ($P < 0.05$). The content of total cholesterol (TCHO) and triglyceride (TG) in the glutinous rice and corn groups was significantly higher than that in high amylose group ($P < 0.05$). The lactic acid (LA) content of the corn group was significantly higher than that of the high amylose group ($P < 0.05$). The LA content of the glutinous rice group was significantly higher than that of the indica rice and high amylose groups ($P < 0.05$). The different sources of starch had no significant effect on high-density lipoprotein (HDL), low-density lipoprotein (LDL), and total protein (TP) ($P > 0.05$).

Table 2. Effects of different starch source diets and time after feeding on blood glucose in geese[1].

Time/min	Blood glucose
-60	9.64[g]
15	12.39[bc]
30	13.43[a]
60	12.97[ab]
120	11.73[cd]
180	11.43[de]
240	10.91[ef]
300	10.30[fg]
360	10.85[ef]
SEM	0.117
Starch source	
Glutinous rice diet	11.86[a]
Corn diet	11.29[ab]
Indica rice diet	11.93[a]
High amylose diet	10.99[b]
SEM	0.117
P-value	
Time	<0.001
Linear	<0.001
Quadratic	<0.001
Starch source	0.010
Time × Starch source	0.490

[a,b]In each row, different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$).
[1]Each value represents the mean of 6 replicate pens.

Serum Hormones

Table 6 shows the effects of different sources of dietary starch on the serum hormones of the 63-day-old geese. These results indicate that the insulin content of the glutinous rice group was significantly lower than that of the corn and high amylose groups ($P < 0.05$). The glucagon content of the glutinous rice group was significantly higher than that of the corn and high amylose groups ($P < 0.05$).

α-Amylase Activity

Table 7 shows the effects of different sources of dietary starch on the pancreas and intestinal α-amylase activity levels of the 63-day-old geese. The results indicated significantly higher α-amylase activity in the pancreas, jejunal chyme, and jejunal mucosa of the glutinous rice group compared to the indica rice and the high amylose groups ($P < 0.05$).

Liver Glucose Metabolism-Related Indexes

Figure 2 shows the effects of different sources of dietary starch on the liver glucose metabolism-related indexes of the 63-day-old geese. As shown in the figure, the liver glycogen content of the glutinous rice group was significantly higher than that of the other groups

Table 3. Interaction of different starch source diets and time after feeding on blood glucose in geese [1]

Time/min	Glutinous rice diet	Corn diet	Indica rice diet	High amylose diet	SEM	P-value
-60	9.77	9.42	10.53	8.85	0.382	0.493
15	13.84[a]	11.90[ab]	12.82[ab]	11.36[b]	0.298	0.039
30	14.98[a]	12.96[b]	13.36[b]	12.40[b]	0.295	0.004
60	14.37	12.37	13.15	12.53	0.340	0.145
120	11.78	11.35	12.25	11.52	0.253	0.642
180	11.17	11.65	11.87	11.05	0.259	0.669
240	10.77	11.00	11.25	10.62	0.214	0.764
300	9.93	10.02	10.97	10.27	0.180	0.161
360	10.98	10.50	11.13	10.32	0.192	0.471

[a,b]In each row, different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$).
[1]Blood glucose concentration of geese at different times after feeding. Each value represents the mean of 6 replicate pens.

Table 4. Effects of different dietary starch sources on growth performance of geese aged 35 to 63 d[1].

Item	Glutinous rice diet	Corn diet	Indica rice diet	High amylose diet	SEM	P-value
35d BW (g)	2,106.07	2,105.92	2,104.38	2,104.40	1.012	0.904
63d BW (g)	3,636.67[ab]	3,678.33[a]	,3701.67[a]	3,593.08[b]	14.725	0.035
ADFI (g)	251.52	254.14	254.58	253.13	1.385	0.884
ADG (g)	54.67[ab]	56.16[ab]	57.05[a]	53.46[b]	0.501	0.041
F/G (g/g)	4.60	4.53	4.47	4.77	0.050	0.246

Abbreviations: ADG, average daily gain; ADFI, average daily feed intake; BW, body weight; F/G, feed/gain.
[a,b]In each row, different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$).
[1]Each value represents the mean of 6 replicate pens.

Table 5. Effects of different starch source diets on serum biochemical indices of 63-day-old geese[1].

Item	Glutinous rice diet	Corn diet	Indica rice diet	High amylose diet	SEM	P-value
Glucose (mmol/L)	15.13[a]	12.96[b]	13.62[b]	12.75[b]	0.277	0.003
TCHO (mmol/L)	8.52[a]	8.16[a]	7.81[ab]	7.11[b]	0.187	0.037
TG (mmol/L)	0.78[a]	0.71[ab]	0.66[bc]	0.56[c]	0.024	0.004
HDL (mmol/L)	4.00	3.82	3.69	3.84	0.072	0.528
LDL (mmol/L)	2.67	2.68	2.61	2.87	0.069	0.601
TP (g/L)	34.75	32.17	33.64	32.72	0.410	0.121
LA (mmol/L)	6.25[a]	5.98[ab]	5.51[b]	4.91[c]	0.138	<0.001

Abbreviations: HDL, high-density lipoprotein; LA, lactic acid; LDL, low-density lipoprotein; TCHO, total cholesterol; TG, triglyceride; TP, total protein.
[a,b,c]In each row, different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$).
[1]Each value represents the mean of 6 replicate pens.

Table 6. Effects of different starch source diets on serum hormones of 63-day-old geese[1].

Item	Glutinous rice diet	Corn diet	Indica rice diet	High amylose diet	SEM	P-value
Insulin (mIU/L)	7.59[b]	8.79[a]	8.12[ab]	8.85[a]	0.186	0.034
Glucagon (ng/L)	1312.83[a]	1085.98[bc]	1194.99[ab]	931.55[c]	42.025	0.004

[a,b,c]In each row, different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$).
[1]Each value represents the mean of 6 replicate pens.

Table 7. Effects of different starch source diets on amylase activities in pancreas and jejunum of 63-day-old geese (U/mgprot)[1].

Item	Glutinous rice diet	Corn diet	Indica rice diet	High amylose diet	SEM	P-value
Pancreas	1.21[a]	1.11[ab]	0.98[b]	0.99[b]	0.033	0.029
Jejunal chyme	0.81[a]	0.73[ab]	0.65[b]	0.66[b]	0.022	0.017
Jejunal mucosa	0.33[a]	0.30[ab]	0.24[b]	0.23[b]	0.014	0.026

[a,b]In each row, values with different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$).
[1]Each value represents the mean of 6 replicate pens.

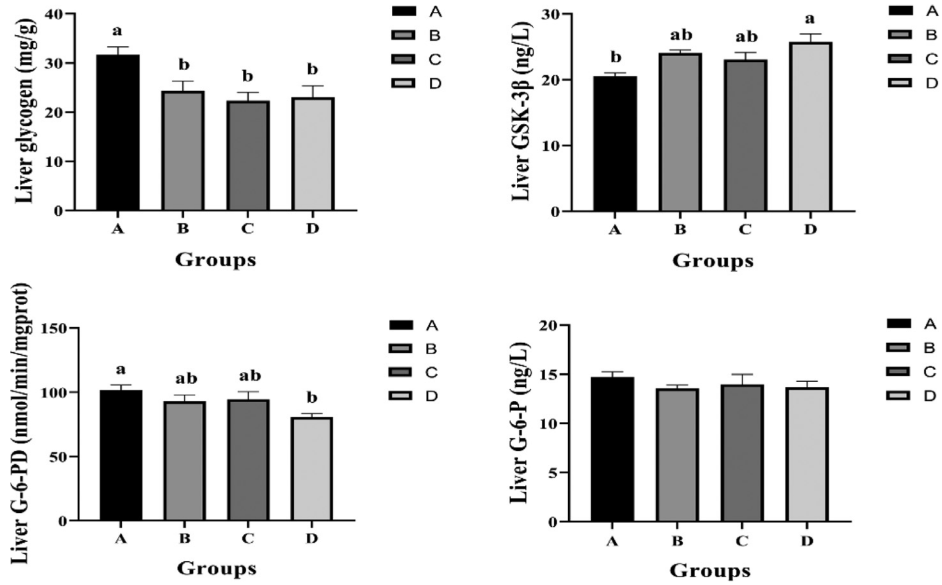

Figure 2. Effects of different starch source diets on liver glucose metabolism- related indexes of 63-day-old geese[1]. [a,b]In each row, different small letter superscripts indicate significant differences ($P < 0.05$), same or no letter superscripts indicate no significant difference ($P > 0.05$). [1] Each value represents the mean of 6 replicate pens. Group A, glutinous rice diet; group B, corn diet; group C, indica rice diet; group D, high amylose diet. GSK-3β, Glycogen synthase kinase-3β; G-6-PD, Glucose-6-phosphate dehydrogenase; G-6-P, Glucose 6 phosphatase.

($P < 0.05$); no significant differences existed between the corn, indica rice, and high amylose groups ($P > 0.05$). The liver GSK-3β content of the high amylose group was significantly higher than that of the glutinous rice group ($P < 0.05$). The G-6-PD activity of the glutinous rice group was significantly higher than that of the high amylose group ($P < 0.05$); no significant differences existed between the corn, indica rice, and high amylose groups ($P > 0.05$). There were no significant differences in liver G-6-P content between the experimental groups.

DISCUSSION

Changes in Blood Glucose

Changes in blood glucose concentration after feeding depend upon the rate at which glucose is released from its conjugates (Riesenfeld et al., 1980). The amylopectin content of glutinous rice starch is high (Guo et al., 2015), resulting in much faster hydrolysis to glucose than in other grains (Lee and Shin, 1998). This experiment yielded results consistent with this observation: compared with the corn, indica rice and high amylose groups, blood glucose increased most rapidly and peaked highest in the glutinous rice group. However, while generally slower rates of increase of blood glucose were observed in the corn, indica rice, and high amylose groups, certain differences were still observed between these groups. Glutinous rice, due its high amylopectin content, can be quickly digested, causing blood glucose levels to increase quickly to a peak and then decreases rapidly. It therefore cannot continuously and stably generate glucose. The blood glucose level in the high amylose group was lower, and also decreased rapidly, because high amylose generally includes a high resistant starch (RS) content. Since RS is scarcely digested in the duodenum, jejunum, or ileum, it is largely digested and utilized by microorganisms in the cecum, where little additional glucose is released from it into the blood. It is worth noting that we found that the blood glucose content for the corn and the indica rice groups remained fairly stable, perhaps because their diets contained more SDS, leading to a continuous, stable release of glucose from the intestine and thus maintaining stable blood glucose levels.

Growth Performance

Since starch is a major component of poultry feed and an important source of energy, its digestion rate can have a significant impact on growth performance. Studies suggest that a continuous, stable release of glucose in the intestine can reduce the oxidation of amino acids in the intestine to supply energy, increasing the synthesis and deposition of protein with a positive effect on the growth of animals (Weurding et al., 2003b). In this experiment the body weights of the corn and indica rice groups at 63 d were significantly higher than that of the high amylose group. From Figure 1, it can also be observed that the energy supply characteristics of the corn and indica rice groups are continuous and stable, maintaining a high level of blood glucose. Consistent with the results of previous studies, this indicates a positive effect of animal growth from sustained, stable intestinal release of glucose. Different cereals differ in terms of starch structure and digestibility (Menoyo et al., 2011; Li et al., 2017;). In this study, the different diets had no significant effect on the feed intake of the geese, indicating that the differences in growth performance were likely caused by differences in the digestibility of the nutrients provided by their different diets.

Blood Biochemistry

Blood biochemical indicators can reflect physical growth and development, health status and nutrient metabolism. Blood glucose levels tend to rise for a short while after animals eat, and in this experiment, those of the glutinous rice group were significantly higher than those of the other groups at 0.5 hours after feeding. This indicates that, compared with the other diets, glutinous rice was more rapidly digested in the intestinal tract, releasing a large amount of glucose and which was quickly transported into the blood. Serum total cholesterol and triglyceride contents provide important information concerning blood lipid metabolism. An intake of rapidly digested carbohydrates increases plasma TG and TCHO concentrations. (Liu et al., 2009; He et al., 2011). Macdonald (1964) believed that compared with corn starch, sucrose would increase serum TG and TCHO concentrations in chickens and rats, since sucrose causes more rapid increases in postprandial blood glucose levels than corn starch. This is consistent with the results of this study. Compared with the corn, indica rice, and high amylose groups, the glutinous rice group had the highest serum TG and TCHO, significantly higher than the high amylose group. Studies have also shown that where the intestinal glucose content is excessively high, the rapidly absorbed glucose is converted into lactic acid in large quantities in the cells of the small intestine, mitigating peak absorption of glucose into the blood (Riesenfeld et al., 1982). The resulting lactic acid is then converted into glucose via gluconeogenesis in the liver. These observations are consistent with the results of this experiment, since the serum lactic acid content of the glutinous rice group was significantly higher than that of the other groups.

Serum Hormones

Insulin and glucagon are both important regulators of glucose metabolism. Insulin is the only hormone in the body that lowers blood glucose levels. The results indicated that the four different sources of dietary starch had significantly different effects on the serum insulin and glucagon levels of the geese. The serum insulin content of the glutinous rice group was significantly lower than for the corn and high amylose groups. Conversely, the glucagon content of the glutinous rice group was significantly *higher* than that of the corn and high amylose groups. This reflects the antagonism of insulin and glucagon: insulin inhibits glucagon secretion (Patel et al., 1982). The blood glucose concentration peak at 0.5 h after feeding in Figure 1 was indicative of a high blood glucose-low insulin response. Studies have shown that this response reflects an increase in insulin secretion at the onset of hyperglycemia (Kawamori and Kulkarni., 2009). Similar results were also obtained in pig studies by Gao et al. (2020). It appears that when blood glucose concentration rises sufficiently rapidly, secreted insulin is unable to suppress it and blood glucose concentration continues to rise without further increases in insulin concentration. Because insulin lowers blood glucose concentrations, as blood glucose is metabolized and consumed, blood insulin then decreases accordingly. Accordingly, the blood insulin concentration begins to increase only after the blood glucose concentration has peaked.

α-Amylase Activity

The intestine is the main organ of digestion and absorption of nutrients in poultry, and starch is an important source from which poultry derive energy (Moran, 1982). In poultry, pancreatic α-amylase is the only enzyme capable of digesting starch; most glucose absorption occurs in the upper small intestine (Riesenfeld et al., 1980), with digestion and absorption of starch mainly in the jejunum (Rogel et al., 1987). The results of this experiment indicated that the α-amylase activities in the pancreas, jejunal chyme, and jejunal mucosa of the glutinous rice group were significantly higher than those of the indica rice and high amylose groups. Research has shown that diets of different starch types affect the enzymatic digestion of starch (Regmi et al., 2011). This may be because glutinous rice starch granules are loose and porous, allowing amylase to enter them easily for hydrolysis (Guo et al., 2015). By contrast, indica rice starch grains have a tight structure and few stomata, so it is not easy for amylase to enter them to cause hydrolysis (Zhou et al., 2014). When starch granules are broken down into disaccharides, their structure loses its compactness, allowing in more amylase to participate in hydrolysis. Glutinous rice contains higher levels of rapidly digestible starch, which is quickly digested by amylase in the intestine, stimulating the pancreas to increase secretion of α-amylase for digestion. The low rapidly digestible starch content of the other diets permitted slow, stable digestion via intestinal amylase, with signals transmitted to the pancreas via the digestive tract regulating secretion of α-amylase.

Liver Glucose Metabolism-Related Indexes

When glucose is in adequate supply, the body stores it in form of glycogen. The conversion of glucose to glycogen is an important way in which blood glucose levels are stabilized. Glycogen is produced when blood glucose exceeds the body's current needs for consumption, and the liver is an important site of glycogen synthesis and storage (Pollock, 2002). In this experiment, the liver glycogen content of the glutinous rice group was significantly higher than the other three groups. This may be because, for geese eating diets containing glutinous rice, blood glucose concentrations increased rapidly by comparison with geese eating other experimental diets. Unable to use so much glucose, their bodies resorted to converting it into glycogen for storage in order to maintain glucose homeostasis. By contrast, the corn, indica rice and high amylose diets, which released glucose slowly, allowed direct utilization of glucose without much conversion into glycogen for storage. Thus the liver glycogen content in these groups was lower.

GSK-3β is a key enzyme involved in hepatic glucose metabolism, which phosphorylates and inhibits glycogen synthase (Steele et al., 2021), thus reducing the synthesis of hepatic glycogen (Embi et al., 1980). In this experiment, the GSK-3β content in the glutinous rice group was significantly lower than that in the high amylose group, an observation which corresponds to the results for hepatic glycogen content. This is likely because decreased GSK-3β content will reduce the phosphorylation of glycogen synthase, which, when glycogen synthase is activated, promotes the uptake and use of blood glucose by hepatocytes for glycogen synthesis, thereby alleviating disordered glucose metabolism and maintaining glucose homeostasis.

Glucose 6-phosphate dehydrogenase (G-6-PD) is a key enzyme in the glucose-catabolic pentose phosphate pathway (Wang et al., 2014). The pentose phosphate pathway directly oxidizes glucose to ribose (5-carbon sugar), meanwhile storing energy in the form of reducing power for use during biosynthesis. Nace and Szepesi (1977) found that feeding a high sucrose diet increased the level of hepatic G-6-PD in rats. In this experiment, hepatic G-6-PD activity was significantly higher in the glutinous rice group relative to the high-amylose group. This indicates that the liver pentose phosphate pathway metabolism in the glutinous rice group was more active relative to the high-amylose group. This may be because, at the time of measurement (0.5 h after feeding), the glucose content in the blood of the glutinous rice group geese was excessive, and glucose was oxidized via the pentose phosphate pathway to maintain blood glucose homeostasis, generating large quantities of NAPDH used in fatty acid and cholesterol synthesis. This is consistent with Table 5 (serum TCHO levels).

G-6-P, a liver-abundant hydrolase, catalyzes the hydrolysis of glucose-6-phosphate to glucose (Nordlie et al., 1993). It releases free glucose in the common terminal reaction of gluconeogenesis and glycogenolysis (Liu et al., 1994), playing an important role in blood glucose homeostasis. The results of this study indicated no significant difference in the effect of the four different diets on liver glucose 6-phosphatase. This may be because, at the time of measurement, the exogenous glucose being absorbed by the intestines was physiologically adequate, eliminating need for release of endogenous glucose. Combined with the liver glycogen content, we speculate that the increase in blood glucose levels at this time is unrelated to hepatic gluconeogenesis, and that increased hepatic glycogen synthesis occurs in order to to alleviate hyperglycemia.

CONCLUSIONS

From this study, it is apparent that the differences in the effects of different dietary starch sources on glucose metabolism start with the digestion of starch in the gut, indicating that starch structure and type are likely major factors influencing glucose metabolism. These thus deserve further study. Under the test conditions, the corn and indica rice diets created a continuous, stable release of glucose, maintaining blood glucose homeostasis with a positive impact on the growth performance of the geese. The diet with excessively high amylose led to an insufficient supply of intestinal energy, reducing the growth of the geese. The glutinous rice diet (rich in rapidly digestible starch) led to rapid release of glucose, reinforcing pathways of glucose metabolism including glycogen synthesis and the pentose phosphate pathway, with further effects on lipid metabolism.

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DISCLOSURES

The authors have no conflicts of interest to report.

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