Effect of Early Feed Restriction on Metabolic Programming and Compensatory Growth in Broiler Chickens[1]

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ABSTRACT The effect of early feed restriction on metabolic programming and compensatory growth was studied in broiler chickens. A total of 480 female 1-d-old broiler birds (Aconred) were randomly allocated to ad libitum and feed-restricted groups, each of which was replicated 6 times with 40 birds per replicate. Broilers were provided commercial diets. Feed-restricted broilers were deprived of feed for 4 h per day from 1 to 21 d of age. Effects of treatments were determined at 21 and 63 d of age. In feed-restricted birds at 21 d of age, BW, average daily gain and average daily feed intake, breast muscle ($P < 0.01$), carcass yield ($P < 0.05$), and abdominal fat ($P < 0.05$) were decreased. Ether extract content in breast muscle was increased ($P < 0.01$), whereas CP content was slightly decreased. Triiodothyronine ($P < 0.01$) and thyroxine ($P < 0.05$) were decreased in serum. Free fatty acid and very low density lipoprotein were slightly increased in serum, whereas triglyceride and glucose were decreased ($P < 0.01$). Activities of NADPH-generating enzymes in liver including malic dehydrogenase, isocitrate dehydrogenase, and glucose-6-phosphate remained unchanged in ad libitum birds, whereas hormone-sensitive lipase activity was increased ($P < 0.01$). In feed-restricted birds at 63 d of age, BW, average daily gain, average daily feed intake, carcass yield, breast muscle yield, and serum triiodothyronine and thyroxine remained as ad libitum birds, whereas abdominal fat yield was increased ($P < 0.05$). Ether extract content in breast muscle was decreased ($P < 0.01$), whereas CP content was increased ($P < 0.05$). Activities of NADPH-generating enzymes were significantly increased, except abdominal malic dehydrogenase and hormone-sensitive lipase activity was decreased ($P < 0.01$) in liver and abdominal fat. Lipoprotein lipase activity was increased ($P < 0.05$) in abdominal fat. In summary, feed restriction severely affected growth performance and lipid metabolism in broilers in the early period. Because there was no statistical difference among the final BW, near full compensatory growth was achieved. In addition, early feed restriction might have induced prolonged metabolic programming in chicks and led to adult obesity.

Key words: feed restriction, lipid metabolism, compensatory growth, metabolic programming, broiler chicken

2007 Poultry Science 86:654–660

INTRODUCTION

Feed restriction has been adopted in broiler production to avoid rapid growth rate, which is associated with ascites, lameness, mortality, and poor reproductive results (Acar et al., 1995; Mench, 2002; Tolkamp et al., 2005). In addition, feed restriction in the early stage is beneficial for improving the feed efficiency and decreasing the breeding cost (Zubair and Leeson, 1994). Although early feed restriction reduces growth performance, compensatory growth in the refeeding period will be attained to accelerate organism growth to reach the weight of animals (Hornick et al., 2000; Pinheiro et al., 2004).

Improved meat quality attracts more and more attention from consumers, and excessive fat deposition is one of the important factors of poor meat quality of broilers. Some studies have shown that feed restriction could decrease fat content and increase protein deposition in carcasses, thus resulting in the improved carcass composition (Jones and Farrell, 1992; Nielsen et al., 2003). However, a lot of research has failed to reduce fat with feed restriction (Zubair and Leeson, 1996; Lippens et al., 2000).

Metabolic programming may be defined as a physiological process whereby early adaptation to a nutritional stress permanently changes the physiology and metabolism of the organism and continues to be expressed even in the absence of the stress that initiates it (Lucas, 1998; Patel and Srinivasan, 2002). It has been reported that early malnutrition leads to metabolic abnormalities later, such

Received July 19, 2006.
Accepted November 24, 2006.
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Table 1. Ingredient composition and nutrient content of diets

Ingredient (g/kg)	Starter (1 to 21 d)	Grower (22 to 42 d)	Finisher (43 to 63 d)
Fish meal	20.0	—	—
Corn	570.0	610.0	650.0
Middlings	40.0	40.0	40.0
Soybean meal	260.0	240.0	185.0
Corn gluten meal	60.0	60.0	70.0
Soy oil	10.0	10.0	15.0
Salt	3.0	3.0	3.0
Monocalcium phosphate	15.0	15.0	15.0
Limestone	12.0	12.0	12.0
Vitamin-mineral premix[1]	10.0	10.0	10.0
Nutrition composition			
ME[2] (kJ/kg)	2,969.4	2,988.5	3,068.3
CP (g/kg)	213.9	195.8	181.5
Ether extract (g/kg)	40.6	40.5	46.4
Ca (g/kg)	9.3	8.5	8.3
Total P (g/kg)	6.6	6.1	5.9
Lys (g/kg)	11.2	10.2	8.7
Met (g/kg)	5.4	4.0	3.4
Met + Cys (g/kg)	9.1	7.6	6.7

[1]Vitamin-mineral premix supplied the following per kilogram of diet: vitamin A, 1,500 IU; vitamin D_3, 200 IU; vitamin E, 10 mg; vitamin K_3, 0.5 mg; thiamine, 1.8 mg; riboflavin, 3.6 mg; D-pantothenic acid, 10 mg; folic acid, 0.55 mg; pyridoxine, 3.5 mg; niacin, 35 mg; cobalamin, 0.01 mg; biotin, 0.15 mg; Fe, 80 mg; Cu, 8 mg; Mn, 60 mg; Zn, 40 mg; I, 0.35 mg; and Se, 0.15 mg.

[2]Value was calculated from data provided by the China Feed Database (1999).

as obesity, glucose (**GLU**) intolerance, and insulin resistance in humans and rats (Martorell et al., 2001; Gonzalez-Barranco and Rios-Torres, 2004; Raatz et al., 2005). However, early malnutrition-induced metabolic programming in broilers is rarely reported.

In the present study, broiler chickens were provided commercial diets. Early feed restriction was performed by removing feed 4 h per day (1400 to 1800 h), and adaption began on the hatching day. Growth performance, carcass characteristics, and lipid metabolism-related enzymes were determined to evaluate the metabolic programming and compensatory growth in broiler chickens after early feed restriction.

MATERIALS AND METHODS

All procedures were approved by the Zhejiang University Institutional Animal Care and Use Committee. Four hundred eighty 1-d-old female Aconred Farms broiler birds, obtained from the local hatchery (Broiler Hatchery of Zhejiang University, Hangzhou, China), were specifically designated to a randomized complete block allocated to 2 treatments (ad libitum group and feed-restricted group), each of which was replicated 6 times with 40 birds per replicate. The chicks were provided the same commercial starter (1 to 21 d), grower (22 to 42 d), and finisher diet (43 to 63 d) according to NRC (1994) recommendations (Table 1). Ad libitum broilers were fed ad libitum, whereas feed-restricted broilers were deprived of feed for 4 h per day (1400 to 1800 h) from 1 to 21 d and then fed ad libitum until the end of the experiment. The chicks were raised in wooden cages (120 × 90 × 50 cm, length × width × height) equipped with nipple waterers and tuber feeders. Water was provided at all times, and continuous lighting was maintained. Temperature was maintained at 32°C for the initial 5 d and then gradually reduced according to normal management practices, until a temperature of 22°C was achieved. Chickens were weighed at 1, 21, and 63 d of age to determine average daily gain (**ADG**). Feed consumed per replicate basis was recorded daily. The uneaten feed was discarded, and fresh feed was replenished. Average daily feed intake (**ADFI**) and feed conversion ratio were determined.

At 21 and 63 d of age, 48 chickens per treatment (8 birds per replicate) were killed for carcass analysis. Birds were randomly selected, deprived of feed for 12 h, weighed, and killed via cardiac puncture. The abdominal fat pad was removed from the body cavity and weighed. The breast muscle was also removed from the body and weighed.

Serum, liver, abdominal fat, and breast muscle were collected and snap-frozen in liquid N. Frozen tissues were stored at –70°C before analysis. The activities of hormone-sensitive lipase (**HSL**), glucose-6-phosphate dehydrogenase (**G-6-PDH**), malic dehydrogenase (**MDH**), and isocitrate dehydrogenase (**ICD**) in liver and abdominal fat were determined as reported before (Xu et al., 2003). Lipoprotein lipase (**LPL**) in abdominal fat was also analyzed according to a previous report (Xu et al., 2003). Serum triiodothyronine (**T_3**) and thyroxine (**T_4**) were measured by RIA according to procedures of the kits (Sigma-Aldrich, St. Louis, MO). Triglyceride (**TG**), GLU, free fatty acid (**FFA**), and very low density lipoprotein (**VLDL**) in serum were determined according to the procedures recommended by the manufacturer of the kits (Nanjing Jiancheng Bioengineering Institute, Nanjing, China). Crude protein and ether extracts (**EE**) in breast muscle were analyzed according to the AOAC (1984).

The experimental data were analyzed by the GLM procedure of SAS software (Windows release 6.04; SAS Institute Inc., Cary, NC) and performed using 1-way ANOVA procedure on files. A value of $P < 0.05$ was considered statistically significant. Data were presented as the means of each treatment. Pooled SEM together with the significant levels of the main effects and interactions were provided. Replicate was considered as the experimental unit for entire index determined.

RESULTS

Growth Performance

Body weight, ADG, and ADFI in feed-restricted broilers were significantly lower ($P < 0.01$) than ad libitum broilers at 21 d of age, whereas no significance was attained concerning feed conversion ratio (Table 2). There were no statistically significant differences between feed-restricted and ad libitum broilers when BW, weight gain, feed intake, and feed conversion ratio were determined at 63 d of age.

Table 2. Effects of early feed restriction on growth performance of female broilers[1]

Item[2]	Ad libitum	Restricted	SEM
BW (g/bird)			
1 d	36.8	37.3	1.38
21 d	459.5	398.3	3.71**
63 d	2,294.0	2,251.6	43.16
ADG[2] (g/bird per d)			
1 to 21 d	20.1	17.2	0.18**
22 to 63 d	43.7	44.1	1.05
1 to 63 d	35.8	35.2	0.68
ADFI[2] (g/bird per d)			
1 to 21 d	34.3	30.0	0.12**
22 to 63 d	118.8	118.8	2.30
1 to 63 d	89.7	88.4	1.49
Feed conversion ratio (g:g)			
1 to 21 d	1.7	1.8	0.02
22 to 63 d	2.7	2.7	0.03
1 to 63 d	2.5	2.5	0.02

[1]Data represent mean values of 6 replicates of each treatment (n = 6).

[2]ADG = average daily gain; ADFI = average daily feed intake.

**$P < 0.01$.

Carcass Composition

As a percentage of BW, abdominal fat ($P < 0.05$), carcass yield ($P < 0.05$), and breast muscle ($P < 0.01$) were significantly lower in restricted broilers at 21 d of age (Table 3). However, no statistical difference in carcass yield and breast muscle was noted at 63 d of age, and abdominal fat in restricted broilers was higher than that of ad libitum broilers ($P < 0.05$).

CP and EE Contents in Breast Muscle

At 21 d of age, EE contents were significantly increased ($P < 0.01$) in the breast muscle of feed-restricted broilers, whereas CP contents showed a tendency to decrease (Table 4). At 63 d of age, EE contents were significantly decreased ($P < 0.01$) in breast muscle of restricted broilers, whereas CP contents were increased ($P < 0.05$).

Serum Metabolites

At 21 d of age, serum TG ($P < 0.01$) and GLU ($P < 0.01$) concentrations were significantly decreased in feed-restricted broilers, whereas FFA and VLDL concentrations were increased (Table 5). At 63 d of age, serum TG ($P < 0.01$) and GLU ($P < 0.01$) concentrations were significantly increased in feed-restricted broilers, whereas FFA ($P < 0.01$) and VLDL ($P < 0.01$) concentrations were decreased.

Activities of Enzymes Related to Lipid Metabolism in the Liver and Abdominal Fat

At 21 d of age, activities of HSL ($P < 0.01$) were increased in the liver of restricted broilers, and activities of MDH, ICD, and G-6-PDH showed an increase. At 63 d of age, activities of MDH ($P < 0.05$), ICD ($P < 0.01$), and G-6-PDH ($P < 0.05$) were increased in the liver of restricted broilers, whereas activity of HSL ($P < 0.01$) was decreased (Table 6).

Because the yield of abdominal fat was too little to be analyzed in feed-restricted broilers at 21 d of age, activities of enzymes related to lipid metabolism were analyzed in abdominal fat of birds at 63 d of age. Results showed that ICD ($P < 0.01$), G-6-PDH ($P < 0.01$), and LPL ($P < 0.01$) activities were increased (Table 7), together with an increase trend in MDH activity, whereas HSL activity was decreased ($P < 0.05$).

Serum T_3 and T_4 Concentrations

Serum T_3 ($P < 0.01$) and T_4 ($P < 0.05$) concentrations in the restricted broilers were lower than those in ad libitum broilers at 21 d of age; however, no significant difference was observed for those between treatments at 63 d of age (Table 8).

DISCUSSION

Feed restriction obviously decreased ADFI and ADG of chicks during 1 to 21 d of age. It is widely accepted that compensatory growth occurs so that animals reach a normal weight once (Hornick et al., 2000; Pinheiro et al., 2004). In the present study, ADFI and ADG were not increased during the refeeding period from 22 to 63 d of age. In addition, ADG was slightly improved in feed-restricted broilers. These results are consistent with many previous reports (Acar et al., 1995; Teguia et al., 2002; Camacho et al., 2004).

Although feed restriction was applied on the hatching day, near full recovery was attained. That might be due

Table 3. Effects of early feed restriction on carcass composition of female broilers[1]

	21 d			63 d		
Item	Ad libitum	Restricted	SEM	Ad libitum	Restricted	SEM
Carcass yield (%)	72.4	70.6	0.46*	75.3	75.4	0.31
Breast muscle (%)	9.7	8.8	0.14**	12.3	12.4	0.24
Abdominal fat (%)	1.06	0.96	0.025*	3.5	4.0	0.14*

[1]Data represent mean values of 6 replicates of each treatment (n = 6). Value was expressed as a percentage of BW just before slaughter.

*$P < 0.05$; **$P < 0.01$.

Table 4. The contents of CP and ether extracts (EE) in breast muscle of female broilers[1]

	21 d			63 d		
Item	Ad libitum	Restricted	SEM	Ad libitum	Restricted	SEM
CP (g/kg)	863.5	859.7	0.38	865.8	876.6	0.32*
EE (g/kg)	38.0	46.2	0.11**	56.6	48.1	0.17**

[1]Data represent mean values of 6 replicates of each treatment (n = 6). Value was calculated on a DM basis.

*$P < 0.05$; **$P < 0.01$.

Table 5. The concentrations of triglyceride (TG), glucose (GLU), free fatty acid (FFA), and very low density lipoprotein (VLDL) in serum of female broilers[1]

	21 d			63 d		
Item	Ad libitum	Restricted	SEM	Ad libitum	Restricted	SEM
TG (mmol/L)	0.36	0.27	0.015**	0.20	0.25	0.010**
GLU (mg/L)	2,900	2,367	71.9**	2,281	2,377	20.93**
FFA (μmol/L)	276.9	326.5	53.6	852.7	642.2	37.81**
VLDL (mg/L)	985	1,020	64.5	816.2	649.8	37.35**

[1]Data represent mean values of 6 replicates of each treatment (n = 6).

**$P < 0.01$.

Table 6. The activities of enzymes related to lipid metabolism in the liver of female broilers[1]

	21 d			63 d		
Item[2]	Ad libitum	Restricted	SEM	Ad libitum	Restricted	SEM
MDH (U/mg of protein)	9.9	10.3	0.13	8.61	9.72	0.27*
ICD (U/mg of protein)	19.7	20.1	1.06	17.2	19.7	0.53**
G-6-PDH (U/mg of protein)	6.4	7.0	0.34	6.1	6.6	0.15*
HSL (U/mg of protein)	19.4	23.6	0.42**	22.5	19.7	0.52**

[1]Data represent mean values of 6 replicates of each treatment (n = 6).

[2]MDH = malic dehydrogenase; ICD = isocitrate dehydrogenase; G-6-PDH = glucose-6-phosphate dehydrogenase; HSL = hormone-sensitive lipase.

*$P < 0.05$; **$P < 0.01$.

Table 7. The activities of enzymes related to lipid metabolism in the abdominal fat of female broilers at 63 d of age[1]

Item[2]	Ad libitum	Restricted	SEM
LPL (U/mg of protein)	11.7	14.2	0.41**
MDH (U/mg of protein)	14.8	16.0	0.72
ICD (U/mg of protein)	19.9	21.2	0.28**
G-6-PDH (U/mg of protein)	5.7	6.5	0.15**
HSL (U/mg of protein)	22.2	17.8	1.19*

[1]Data represent mean values of 6 replicates of each treatment (n = 6).

[2]LPL = lipid lipoprotein; MDH = malic dehydrogenase; ICD = isocitrate dehydrogenase; G-6-PDH = glucose-6-phosphate dehydrogenase; HSL = hormone-sensitive lipase.

*$P < 0.05$; **$P < 0.01$.

Table 8. The concentrations of triiodothyronine (T_3) and thyroxine (T_4) in the serum of female broilers[1]

	21 d			63 d		
Item	Ad libitum	Restricted	SEM	Ad libitum	Restricted	SEM
T_3 (ng/mL)	2.1	1.7	0.03**	1.0	1.1	0.04
T_4 (ng/mL)	60.5	55.3	0.77*	65.7	63.3	0.87

[1]Data represent mean values of 6 replicates of each treatment (n = 6).

*$P < 0.05$; **$P < 0.01$.

to the lower intensity of early feed restriction. In addition, there was not significant difference concerning feed conversion ratio between feed-restricted and ad libitum broilers. These results are consistent with previous reports (Zubair and Leeson, 1994; Palo et al., 1995; Camacho et al., 2004).

Feed restriction reduces the growth rate of tissues, and some tissues (adipose tissue) react more sensitively (Hornick et al., 2000). In our present study, feed restriction during 1 to 21 d of age severely decreased the carcass yield and breast muscle and fat deposition in abdomen. That might be due to fat mobilization for energy supply, and abdominal fat might be mobilized more easily during a fasting period. There were no significant differences concerning carcass yield and breast muscle between 2 treatments at 63 d of age. The results indicate that full compensatory growth was attained during the refeeding period, which is consistent to the previous reports (Camacho et al., 2004; Teimouri et al., 2005).

Thyroid hormones, including T_3 and T_4, are recognized as the key metabolic hormones of the body, with T_3 being the most functionally active form. The majority of circulating T_3 is derived from the deiodination of T_4 in nonthyroidal tissues such as the liver and kidney (Smith et al., 2002). The serum level of thyroid hormones is associated with protein synthesis and energy production (Hornick et al., 2000; Smith et al., 2002). In the present study, during the feed restriction period, there was a lower concentration of thyroid hormones in feed-restricted broilers. This might be caused by the low basal metabolism and thus allows the organism to spare energy by decreasing basal metabolism (Hornick et al., 2000). However, there was not statistical significance between 2 treatments concerning the thyroid hormones levels during the refeeding period. Results indicate that T_4 and T_3 levels of the restricted chicks are normalized and remain as the value of ad libitum broilers during compensatory growth. In summary, levels of thyroid hormones are closely correlated with growth performance and shift the energy metabolism of broilers.

The amount of abdominal fat was significantly increased during the refeeding period, and broilers looked much more fatty and obese in restricted broilers at 63 d of age. This suggests that feed-restricted chickens tend to enhance fat deposits during the refeeding period. In previous studies concerning early feed restriction, some reported a decreased trend for fat deposition (Jones and Farrell, 1992; Nielsen et al., 2003), whereas others reported opposite results (Zubair and Leeson, 1996; Lippens et al., 2000). The discrepancies might be due to the metabolic programming whereby early malnutrition leads to adult life obesity. The metabolism programming is induced by nutritional experience during the critical period in development with consequences later in adulthood (Lucas, 1998; Patel and Srinivasan, 2002). It has been reported in humans that the tendency to store abdominal fat might be a persisting response to adverse conditions and growth failure in fetal life and infancy (Law et al., 1992; Martorell et al., 2001; Gonzalez-Barranco and Rios-Torres, 2004). The first week of life in chickens is the critical stage because of the sensitive influence of dietary composition and higher requirements to maintain a higher metabolic rate (Camacho et al., 2004). In the present study, early feed restriction was applied on the hatching day for 1 to 21 d of age, which might have prolonged positive effects on lipid metabolism, abdominal fat deposition, and thus result in adult obesity. In summary, the initial day, long period, and lower intensity of early feed restriction might induce metabolism programming, thus contributing to excessive fat deposition in adult life of broilers. However, compensatory growth was not affected when the feed restriction was cancelled.

At 21 d of age, compared with the ad libitum broilers, EE content of breast muscle was increased in feed-restricted broilers, whereas the CP content remained the same as ad libitum broilers. That indicates that fat content in muscle, lipid stored intracellularly and interfasciculi, is widely elevated. In addition, GLU and TG concentrations in serum were significantly decreased, whereas FFA concentration in serum was increased in feed-restricted broilers. It is wildly accepted that the major fuels of muscle are GLU, fatty acids, and ketone bodies (Kokta et al., 2004). Fatty acids in muscle are derived from plasma FFA, circulating TG, and endogenously stored i.m. TG (Cortright et al., 1997). The present study indicated that fatty acids tended to be transferred from abdomen to intramuscle, causing increased levels of i.m. lipid deposition. This became a major energy provider for muscle during the feed-restricted period. The results are inconsistent with previous reports (Gondret et al., 2000; Gondret and Lebret, 2002). The discrepancies might be due to the lower intensity of feed restriction applied to birds in our experiment.

At 63 d of age, EE content of breast muscle was decreased, whereas CP content was increased in feed-restricted broilers. This indicates that early feed restriction tended to increase the yield of muscle during the refeeding period. In addition, GLU and TG in serum were significantly increased, whereas FFA was significantly decreased. These results are consistent with previous reports for obesity characteristics (Gonzalez-Barranco and Rios-Torres, 2004; Caldeira et al., 2007). The higher level of GLU and TG might be due to the enhanced insulin resistance and reduced GLU tolerance caused by the metabolic programming for early malnutrition.

In the present study, it was obvious that early feed restriction severely affected the lipid metabolism. Lipogenic and lipolytic enzymes in liver and abdominal fat were determined to reveal the mechanism of lipid metabolism in different treatments. Malic dehydrogenase, ICD, and G-6-PDH are responsible for generating NADPH for the support of lipogenesis. Hormone-sensitive lipase has the opposite effect of mobilizing fatty acids from adipocytes into the bloodstream in the process of lipolysis. Lipoprotein lipase, in adipose tissue, is involved in the movement of fatty acids from TG in blood chylomicrons and VLDL to the adipocytes (Gondret et al., 2000; Xu et al., 2003; Kokta et al., 2004; Pashkov et al., 2005). At 21 d of age, there were no statistical significances between feed-restricted and ad libitum broilers concerning NADPH-generating enzymes (MDH, ICD, and G-6-PDH) activity in the liver of broilers, whereas HSL activity was much higher in restricted broilers. Lipid metabolism-related enzymes in abdominal fat were not analyzed because of the little yield of abdominal fat in restricted broilers. At 63 d of age, NADPH-generating enzymes activities were significantly increased in liver and abdominal fat of the restricted broilers, whereas HSL activity was significantly decreased. It is obvious that changes of serum FFA concentration and abdominal fat yield are closely associated with patterns of HSL and NADPH-generating enzymes. The enzymatic machinery of liver and abdominal adipocyte has adapted in such a way as to increase or decrease the capacity for NADPH generation for fatty acid synthesis and mobilization of fatty acids from abdominal adipocytes, thereby facilitating the use of energy toward maintenance and growth processes. In addition, the elevated level of LPL activity improved the movement of fatty acids from TG and VLDL in the bloodstream to adipocytes and thus increased the abdominal fat deposition.

In summary, early feed restriction during 1 to 21 d of age obviously altered the growth performance and lipid metabolism. When feed restriction was cancelled in the grower and finisher period from 22 to 63 d of age, near full compensatory growth was attained. However, broilers were much more fatty and obese in feed-restricted broilers and had significantly elevated levels of lipid synthesis. The first week of life in broilers is the critical stages. So, the initial day, long period, and early feed restriction might induce the prolonged metabolic programming in chicks, thereby resulting in obesity in adult life. The insights presented in the present study set a new direction of understanding the mechanism of early feed restriction effects on broiler chickens and would be helpful for avoiding obesity-related problems during broiler production and exploring ways of improving meat quality of broilers.

ACKNOWLEDGMENTS

Financial support provided by the National Basic Research Program of China (project 2004CB117505) is gratefully acknowledged.

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