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Assessment of De-Novo Fatty Acid Synthesis in Broiler Chickens Fed Diets Containing Different Mixtures of Beef Tallow and Soybean Oil

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Abstract: Replacement of dietary saturated fatty acids (SFA) by polyunsaturated fatty acids (PUFA) has been consistently shown to reduce the amount of abdominal fat in broiler chickens, but the metabolic basis for this effect is unknown. It was hypothesized that the feeding of PUFA instead of SFA would inhibit whole-body de novo fatty acid synthesis. As indexes of de novo fatty acid synthesis, we used the concentration of plasma triacylglycerols and minimum fatty acid synthesis calculated as fatty deposition minus digestible fatty acid intake. Broiler chickens were given one of five diets in which the beef tallow component, which is rich in SFA, was replaced by increasing amounts of soybean oil, which is rich in PUFA. The variable fat content of the diets was 3% (w/w). There were neither significant nor systematic effects on weight gain and feed:gain ratio. The amount of abdominal fat was reduced significantly when about 75% of the tallow was replaced by soybean oil, but there was no further decrease after the incorporation of more soybean oil into the diet. The decrease in abdominal fat was associated with a decrease in the level of plasma triacylglycerols, but it was not associated with minimum de novo fatty acid synthesis in the whole body.

Key words: Dietary fatty acids, broilers, abdominal fat, fatty acid deposition, fatty acid synthesis

Introduction

Numerous investigations have demonstrated that substitution of dietary polyunsaturated fatty acids (PUFA) for saturated fatty acids (SFA) reduces the amount of abdominal fat in broilers (Sanz et al., 1999, 2000a; Crespo and Esteve-Garcia, 2002; Newman et al., 2002; Pinchasov and Nir, 1992; Villaverde et al., 2005; Zollitsch et al., 1997; Wongsuthavas et al., 2007). The mechanism underlying the diminishing effect of PUFA on abdominal fat mass is not known (Crespo and Esteve-Garcia, 2002bc, 2003; Newman et al., 2002; Villaverde et al., 2006; Sanz et al., 2000b). We have put forward (Wongsuthavas et al., 2007a) the following possible mechanism. PUFA versus SFA acids are preferentially oxidized (Beynen and Katan, 1985) and thereby yield ATP so that carbohydrates are shifted from the oxidative into the lipogenic pathway. The conversion of glucose into triglycerides is less efficient in terms of energy deposition than is the conversion of fatty acids into triglycerides (Newsholme and Leech, 1994). As a consequence, the feeding of PUFA instead of SFA would not only lead to less deposition of abdominal fat, but be associated with more heat expenditure. However, we had to reject our hypothesis on the basis of a recent experiment in which energy expenditure was calculated for broilers fed on diets with different PUFA:SFA ratios (Wongsuthavas et al., 2007b).

An alternative hypothesis explaining the observed PUFAinduced reduction in abdominal fat in broiler chickens would be inhibition of de-novo fatty acid synthesis. There is evidence that the feeding of PUFA instead of SFA will inhibit de-novo fatty acid synthesis in the body (Zheng et al., 2006; Sanz et al., 2000b; Ide et al., 1996; Clarke et al., 1976). In this study, we tested whether a PUFAmediated reduction in abdominal fat mass would be associated with a decrease in whole-body fatty acid synthesis. Broiler chickens were fed on diets in which the beef tallow component, which is rich in SFA, was replaced by increasing amounts of soybean oil, which is rich in PUFA. Whole-body fatty acid synthesis was assessed indirectly by using two indicators. First, we measured the concentration of plasma triacylglycerols. Studies with isolated hepatocytes indicate that the concentration of plasma triacylglycerols is an index of de-novo fatty acid synthesis (Beynen et al., 1983). Secondly, we calculated minimum de-novo fatty acid synthesis as fatty deposition in whole carcass minus digestible fatty acid intake.

Materials and Methods

Animals and experimental diets: Seven-day-old Arbor Acres broiler chicks were randomly allocated to five groups of 15 birds each and kept in individual cages.

Table 1: Ingredient and analyzed composition of the experimental diets

	Diet code							
Item	1	2	3	4	 5			
Ingredients (g/100 g diet)								
Tallow	2.87	1.45	0.72	0.28	-			
Soybean oil	0.13	1.56	2.28	2.72	3.00			
Constant components	97.00	97.00	97.00	97.00	97.00			
Macronutrients (g/100 g diet)								
Dry matter	92.0	91.8	91.98	91.98	91.98			
Crude Protein	18.0	18.0	18.1	18.1	18.0			
Crude fat	3.4	3.5	3.4	3.3	3.3			
Crude fiber	3.2	3.3	3.2	3.2	3.2			
Ash	4.3	4.3	4.3	4.3	4.3			

The constant components consisted of (g/100 g diet): tapioca starch, 46.02; soybean meal, 41.05; rice bran hulls, 4; dicalcium phosphate, 3.87; D,L-methionine, 0.3; L-lysine, 0.25; sodium chloride, 0.51; premix, 1. The premix supplied per kg of diet: vitamin A, 1,650 IU; vitamin D, 330 IU; vitamin E, 11 IU; vitamin K, 0.55 mg; thiamine, 198 mg; riboflavin, 3.96 mg; niacin, 3.30 mg; pyridoxine, 3.85 mg; vitamin B_{12} , 0.01 mg; calcium pantothenic acid, 10 mg; folacin, 0.61 mg; biotin, 0.17 mg; choline, 1,430 mg; manganese, 65.99 mg; iodine, 0.39 mg; potassium, 330 mg; zinc, 43.97 mg; copper, 8.80 mg; ferrous, 87.59 mg; selenium, 0.17 mg

Table 2: Fatty acid composition of the diets

Fatty acid	Diet cod	Diet code							
composition, %	1	2	3	4	5				
C16:0	27.63	26.31	26.48	26.50	25.61				
C18:0	32.47	23.45	16.26	11.55	7.95				
C18:1 n-9	9.06	16.56	15.74	16.24	15.81				
C18:1 n-7	2.69	2.79	2.09	1.68	1.45				
C18:2 n-6 c	8.11	11.02	15.44	16.00	19.70				
C18:3 n-6	0.40	0.26	0.00	0.00	0.00				
C18:3 n-3	1.13	1.52	2.03	2.09	2.65				
ΣSFA	68.31	55.38	48.09	45.50	41.33				
ΣMUFA	15.93	26.47	28.92	32.04	31.91				
ΣPUFA	9.64	12.80	17.47	18.09	22.35				

ΣSFA= C8: 0+ C10: 0+ C12: 0+ C14: 0+ C15: 0+ C16: 0 + C17: 0+ C18:0+C20:0+C22:0+C24:0; ΣΜUFA= C14: 1+ C15: 1+ C16: 1+C18:1n-9+C18:1n-7+C20:1n-9; ΣΡUFA=C18:2 n-6+18:3 n-6+18:3 n-3

The five experimental diets were formulated to contain 3% of added fat. As indicated in Table 1, the amount of soybean oil was increased stepwise at the expense of beef tallow. Fatty acid composition of the experimental diets is shown in Table 2. The birds had free access to feed and water.

Data and sample collection: The chickens were weighed at 7 and 28 days of age. Feed consumption was recorded daily. The feed:gain ratio was calculated (g feed/g gain). Excreta were collected quantitatively during the entire experimental period. At the age of 28 days, the birds were stunned and killed. The birds were killed at 08.00 am after a three-hour fasting period. Five birds per treatment were randomly chosen for weight measurement of abdominal adipose tissue (from the proventriculus surrounding the gizzard down to the cloaca) and blood sampling. The remaining 10 birds per dietary treatment were used to measure fatty acid composition of whole carcass.

Chemical analysis: The experimental diets were analyzed for dry matter, ash, crude fat, crude fiber and

crude protein (AOAC, 1985). Total fat in dried excreta and carcass were extracted as described previously (Horwitz, 1975). Each sample was added to a flask and 2 ml of ethanol was added. Subsequently, 10 ml of HCl (8 mol/L) was added; the contents were gently mixed and the flask was placed in a water-bath of 80°C for 30-40 min. The tubes were cooled down, 10 ml of ethanol (96%, w/w) and 25 mL of petroleum ether (boiling point between 40 and 60°C) were added and the tube was shaken for one min. The fat-containing upper layer was decanted into a 150-mL round-bottom flask. The extraction procedure was repeated twice with 15 mL of diethyl ether and 15 mL of petroleum ether and the lipid extract was evaporated to dryness under N₂ in a waterbath of 40°C. The round-bottom flasks with the lipids were dried overnight at 60°C and the total lipids were measured gravimetrically. Total lipids were saponified and methylated according to the procedure of Metcalfe et al. (1966) followed by gas chromatography for determination of fatty acid composition. Concentrations of plasma triacylglycerols and cholesterol were analyzed according to the procedure of (Javadi, 2005).

Calculation of digestible fatty acid intake, fatty acid deposition and minimum de novo synthesis: The total digestible fatty acid intake was calculated as fatty acid intake (g/21 days) × apparent fatty acid digestibility (fraction of intake). The deposition of fatty acids was calculated with the following formula: Fatty acid deposition (g/21 days) = carcass content of fatty acid at the end of the study-carcass content of fatty acid at the start of the study. To determine baseline body fatty acid content, ten 7-day old chickens were used and their values were averaged. The ratio of fatty acid deposition and digestible fatty acid intake was calculated for selected individual fatty acids and groups of fatty acids. Minimum de novo fatty acid synthesis was calculated as fatty deposition minus digestible fatty acid intake.

Table 3: Effects of experimental diets on growth performance and weight of abdominal fat tissue

	Diet code	Diet code					
Item	1	2	3	4	5	SE	
Initial BW, g	184	176	182	187	182	4.10	
Final BW, g	655	668	613	631	647	9.80	
ADFI, g	45.4	47.2	44.8	42.4	41.8	3.00	
ADG, g	22.4	23.4	21.0	21.8	22.1	2.38	
Feed : gain	2.07	2.02	2.18	2.04	1.80	0.63	
Abdominal fat, % of final BW	1.19ª	1.07°	0.81⁵	0.88 ^b	0.94⁵	0.27	

^{a-b}Means in the same row with different letters are significantly different (p<0.05); Performance data are for 15 birds per dietary treatment. Abdominal fat data are for 5 birds per dietary treatment

Table 4: Influence of experimental diets on blood plasma lipid concentration

	Diet code					
Blood plasma						
lipid concentration	1	2	3	4	5	P ∨alue
Cholesterol, µmol/l	3,650	3,435	3,356	3,144	2,794	0.069
Triacylglycerols, µmol/l	2,751°	2,110⁵	2,092b	2,106b	1,985 ^b	0.016

^{a-b}Means in the same row with different letters are significantly different (n = 5)

Table 5: Influence of increasing levels of PUFA on fat and fatty acid deposition in whole carcass

Item	Diet code						
	1	2	3	4	5	P ∨alue	Pooled SE
Fat deposition i	n final whole carc	ass, %					
	27.97	27.48	26.13	26.63	25.74	0.6086	3.5541
Fatty acid comp	osition, % of who	le carcass					
C16:0	24.59°	23.49ab	23.15 ^b	24.74ª	22.90⁵	0.0080	1.3424
C18:0	20.53°	18.54 ^b	17.19 ^b	9.81⁰	7.72 ^d	0.0001	1.7648
C18:1 n-9	37.93b	40.46°	40.79°	40.76°	31.90⁰	0.0001	1.2936
C18:2 n-6	8.06≎	11.19 ^b	11.66⁵	12.00b	13.73°	0.0001	1.2329
C18:3 n-3	0.39 ^d	0.71⁵	0.72⁰	0.82 ^b	0.88	0.0001	0.0650
Σ SFA	45.38°	42.29b	40.61 ^b	34.81⁰	30.80 ^d	0.0001	2.3043
ΣMUFA	43.93b	46.80°	46.89°	46.64°	37.88°	0.0001	1.7093
$\sum_{i=1}^{n} PUFA$	9.13⁰	12.21b	12.89b	13.01b	14.35°	0.0001	1.2886

a-b-c-dMeans in the same row with different letters are significantly different (n = 10)

Statistical analysis: Data were subjected to Duncan's multiple range test (Steel and Torrie, 1980) using the program of Microsoft Excel (Windows XP[®]). The level of statistical significance was preset at p<0.05.

Results and Discussion

keeping with our previous investigation (Wongsuthavas et al., 2007a), there were no significant diet effects on weight gain, feed intake and feed:gain ratio (Table 3). The amount of abdominal fat was reduced significantly (p<0.05) when about 75% of the tallow was replaced by soybean oil. Contrary to our earlier work (Wongsuthavas et al., 2007a), there was no further decrease after the incorporation of more soybean oil into the diet. The lowering of abdominal fat was in the order of 20-30%. Thus, this study confirms the wellknown effect that substitution of PUFA for SFA in the diet of broiler chickens diminishes the deposition of

The concentration of triacylglycerols in plasma was measured as an index of de-novo fatty acid synthesis. Table 5 illustrates that the replacement of beef tallow by

soybean oil caused a significant reduction in plasma triacylglycerols (p<0.05). The reduction was already maximal when the diet with lowest inclusion level of soybean oil was fed. A decrease in plasma triacylglycerols after substitution of dietary PUFA for SFA has been observed earlier in broiler chickens (Crespo and Esteve-Garcia, 2001; Crespo and Esteve-Garcia, 2003). Thus, in this study the decrease in abdominal fat associated with a lowering of plasma triacylglycerols. The implication could be that the diminished deposition of abdominal fat was caused by inhibition of de-novo fatty acid synthesis. The replacement of tallow by soybean oil produced a doseof plasma dependent lowering cholesterol concentrations (Table 4). This observation confirms earlier work (Newman et al., 2002).

Table 5 shows that the total SFA and PUFA content of whole carcass differed between the dietary groups. The replacement of SFA by PUFA lowered the SFA content of the whole body and increased that of PUFA. Other investigators have also reported that replacement of dietary SFA by PUFA had marked effects on total body

Table 6: Individual fatty acid digestibility, g/100g fatty acid intake

Item	Diet code							
	1	2	3	4	 5	P ∨alue		
Fatty acid comp	osition							
C16:0	73.85 ^b	76.69 ^b	81.30°	80.49°	81.40°	0.0001		
C16:1	42.58b	50.12⁵	25.34b	63.51°	60.34°	0.0001		
C18:0	69.77	71.87	75.04	73.40	72.71	0.1852		
C18:1 n-9	75.42b	82.80°	82.69°	80.55°	79.48°	0.0001		
C18:2 n-6	82.02b	76.29⁰	83.89ab	82.09b	85.46°	0.0001		
C18:3 n-3	79.72 ^b	73.94⁰	85.67°	81.24 ^b	85.79°	0.0001		
ΣFA	73.77°	75.90 ^d	80.18 ^b	79.26⁵	80.44°	0.0001		
∑SFA	72.29b	73.73 ^b	78.04ª	78.29°	79.70°	0.0005		
$\sum_{i=1}^{n} MUFA$	77.16⁵	80.25 ^a	76.04 ^b	81.42°	79.69°	0.0001		
∑PUFA	80.87b	75.12⁰	84.78°	81.67⁵	85.63°	0.0001		
$\sum_{i=1}^{n}$ UFA	76.96⁰	79.81₺₢	83.56°	81.66ab	82.55ab	0.0004		

a-b-c-d-eMeans within a row with different superscripts differ significantly; n = 15

fatty acid composition (Pinchasov and Nir, 1992; Crespo and Esteve-Garcia, 2002). The UFA were the predominant fatty acids in whole carcass for all of the treatments. However, for the diet with the highest PUFA level, PUFA deposition in the whole body was higher than for the other dietary groups (Table 5).

The dietary fat type had marked effects on the apparent digestibility of individual fatty acids. Palmitic, oleic, linoleic and alpha-linolenic acid were digested more efficiently when present in soybean oil than in beef tallow. A combination of different factors may be responsible for the observed diet-induced differences in apparent digestibility of identical fatty acids. As mentioned above, the total crude fat digestibility for soybean oil was greater than that for beef tallow, which may relate to enhanced micelle formation after feeding soybean oil. An improved micelle formation may favorably influence the digestion of all fatty acids in the diet. The position of a given fatty acid in the triacylglycerol molecule also plays a role. Fatty acids at the 2 position of glycerol in triacylglycerol molecules are better digested than those at the 1,3 position (Bracco, 1994; Innis and Dyer, 1997; Nelson and Innis, 1999). During digestion, the pancreatic lipase action specifically removes fatty acids at the 1.3 position while the resulting monoacylglycerol molecule is efficiently incorporated into micelles (Lien, 1994), leading to preferential absorption of fatty acids at the 2 position of the glycerol backbone of triacylglycerols. The intake level of a given individual fatty acid and its faecal excretion of endogenous origin will also affect the calculated apparent digestibility. A low intake level in combination with a high endogenous excretion will by itself lead to a low apparent digestibility. When comparing the digestibilities of palmitic and stearic acid for the diets with soybean oil and beef tallow, the values for the diets with soybean oil diet may biased to lower values because the intake levels were lower. On the other hand, the apparent digestibility for linoleic acid on the diets rich in soybean oil diet may be biased towards a higher value (Table 6).

The calculated intake of digestible fatty acids reflects the amount in the diet and feed intake, combined with the measured apparent digestibility. The deposition in the body of fatty acids was calculated as based on the fatty acid composition of the total body fat that was gained during the entire feeding period. As would be expected, the chickens fed the diets rich in soybean oil deposited more linoleic acid and those fed on diets rich in beef tallow had deposited more stearic acid in their whole body. Similar data have been shown for mice (Javadi et al., 2005) and goats (Yeom et al., 2005). The increased deposition of palmitic acid in the birds fed the diet rich in beef tallow did not reach statistical significance (Table 7).

To obtain clues as to preferential deposition of fatty acids, the ratio of deposition of a given fatty acid or group of fatty acids to the intake of digestible fatty acid or group of fatty acids was calculated. The deposition:intake ratio for fatty acid reflects the net amount synthesized and/or the proportion of the digested fatty acid not oxidized. A deposition:intake ratio>1 would point at net de novo synthesis, whereas a ratio<1 would indicate net oxidation. The low deposition: intake ratio for linoleic acid in the chickens fed the diets rich in soybean oil is consistent with the well-known preferential oxidation of linoleic acid (Slim et al., 1996; Sanz et al., 1999; Sanz et al., 2000b) and the fact that linoleic acid cannot be synthesized by chickens (Schafer et al., 2001). The deposition:intake ratio for the essential polyunsaturated fatty acids, linoleic and alpha-linolenic acid, cannot be higher than 1. Indeed, the ratios for alpha-linolenic acid were below and so was the ratio for linoleic acid in the broilers fed diets rich in soybean oil. The chickens fed diets high in beef tallow had a group mean deposition:intake ratio for linoleic acid that was just above 1, but was not significantly higher than 1. The extremely high deposition:intake ratio for stearic acid in chickens fed diets high in soybean oil is explained by a relatively low intake and high net synthesis of this fatty acid as shown in Table 7.

Wongsuthavas et al.: De-Novo Fatty Acid Synthesis in Broiler

Table 7: Effect of dietary fat type on digestible fatty acid intake, fatty acid deposition, deposition:intake ratio and minimum de-novo fatty acid synthesis during the whole feeding period

latty dore	Diet code	ring the whole leed					
Fatty acids							Pooled
	1	2	3	4	5	P ∨alue	SE
Digestible intake, ga	/21 days						
C16:0	3.47°	2.76⁵	2.74 ^b	2.37⁰	2.17 ^c	0.0001	0.2840
C18:0	6.62°	3.35⁵	2.18⁵	1.18 ^d	0.61°	0.0001	0.3135
C18:1 n-9	5.94°	5.59⁵	5.61⁵	5.30°	5.28°	0.0001	0.1484
C18:2 n-6 c	2.02°	8.27 ^d	11.24°	12.40b	13.70°	0.0001	0.1821
C18:3 n-3	0.13°	0.52 ^d	0.74°	0.80 ^b	0.88ª	0.0001	0.0242
∑FA	23.87 ^{ab}	23.25b	24.42°	23.13b	23.25 ^b	0.0491	1.0798
$\overline{\Sigma}$ SFA	10.19 ^a	6.32 ^b	5.20°	3.84 ^d	3.10°	0.0001	0.5892
∑MUFA	6.25°	5.87⁵	5.90⁵	5.56⁵	5.53⁵	0.0001	0.1645
$\sum_{i=1}^{n} PUFA$	2.33°	9.05⁴	12.03°	13.25⁵	14.63°	0.0001	0.2036
Deposition, g/21 da	ys						
C16:0	5.96°	5.83°	4.15⁵	5.09ab	4.52°	0.0159	1.3554
C18:0	6.09°	5.91°	4.24b	1.99⁵	1.28⁵	0.0001	0.8604
C18:1 n-9	8.55ab	10.04°	7.44 ^b	8.15 ^{ab}	5.15°	0.0001	2.0188
C18:2 n-6	1.99⁰	3.31ab	2.72⁵	3.03⁵	3.69ª	0.0001	0.6718
C18:3 n-3	0.06°	0.20°	0.15⁵	0.20°	0.22ª	0.0001	0.0447
∑FA	23.74ab	24.93°	18.30⁰	20.04 ^{bc}	20.37 ^{bc}	0.0147	4.6774
$\overline{\Sigma}$ SFA	12.11 ^a	11.81 ^a	8.44 ^b	7.14 ^{bc}	5.83°	0.0001	2.1086
∑MUFA	9.89ab	11.59°	8.50⁵	9.24b	6.28⁵	0.0003	2.3810
$\sum_{i=1}^{\infty} PUFA$	2.27°	3.57 ^{ab}	2.99⁵	3.24 ^{ab}	3.78°	0.0001	0.6825
Deposition : intake,	g/21 days						
C16:0	1.72 ^{ab}	2.12°	1.55⁵	2.18°	2.08°	0.0417	0.5399
C18:0	0.92⁵	1.77 ^{ab}	1.98°	2.04°	2.32ª	0.0458	1.0361
C18:1 n-9	1.44 ^b	1.80°	1.33 ^b	1.54 ^{ab}	0.97⁰	0.0003	0.3729
C18:2 n-6	0.99°	0.40⁵	0.24⁵	0.24⁵	0.27⁰	0.0001	0.1238
C18:3 n-3	0.51°	0.37⁵	0.20⁵	0.25⁵	0.25⁰	0.0001	0.1245
Σ FA	0.99ªb	1.07°	0.75⁵	0.87 ^{bc}	0.87 ^{bc}	0.0070	0.1952
Σ SFA	1.19⁵	1.88°	1.65°	1.93°	1.88ª	0.0129	0.5170
$\sum_{i=1}^{n} MUFA$	1.58b	1.98°	1.45 ^{bc}	1.66ab	1.13 ^c	0.0011	0.4201
$\sum_{i=1}^{n} PUFA$	0.98°	0.39⁵	0.25⁵	0.25⁵	0.26⁰	0.0001	0.1080
Minimum de novo f							
SFA	1.92⁵	5.49°	3.24b	3.30 ^b	2.73 ^b	0.0087	2.0348
MUFA	3.64b	5.72ª	2.60b	3.68b	0.75b	0.0063	2.1975
SFA/(SFA+MUFA)	0.35 ^b	0.49ª	0.55°	0.47 ^{ab}	0.78°	0.0022	0.2275

a-b-c-d-eMeans within a row with different superscript differ significantly; n = 15

The birds fed soybean oil instead of beef tallow had a higher deposition:intake ratio for SFA, but lower ratios for MUFA and PUFA. The diet effect on the ratios for SFA and MUFA can be explained by the calculated minimum synthesis of these groups of fatty acids. Feeding the diet containing soybean oil stimulated the synthesis of SFA, but depressed that of MUFA. The higher synthesis ratio for SFA: (SFA+MUFA) in chickens fed the diets rich in soybean oil indicates that there was selective synthesis of SFA in these birds. This might point at de novo fatty acid synthesis being regulated to balance the amount of saturated and unsaturated fatty acids in the body because the intake of linoleic acid was very high in the birds fed the diets rich in soybean oil (Table 7).

In conclusion, the gradual replacement of beef tallow by soybean oil had no effect growth performance, but rather improved the digestibility of all individual fatty acids. Feeding the diets with increasing levels of soybean oil produced a markedly increased deposition of linoleic acid in the whole body. For groups of fatty acids, the ratio

of deposition in the whole body to the intake of digestible fatty acids was calculated. It then became clear that the type of dietary had marked, specific effects on the synthesis and oxidation of fatty acids. The decrease in abdominal fat as induced by the feeding of soybean oil instead of beef tallow was associated with a decrease in plasma triacylglycerol concentrations, but not with a decrease in calculated minimum de novo fatty acid synthesis.

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Wongsuthavas et al.: De-Novo Fatty Acid Synthesis in Broiler

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