Nutrient and Fatty Acid Deposition in Broilers Fed Different Dietary Fatty Acid Profiles

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ABSTRACT The aim of this study was to determine the effect of different dietary fatty acid profiles on efficiency of energy, fat, nitrogen, and fatty acid deposition in broiler chickens. Sixty female broiler chickens were fed a basal diet without additional fat or with 4 other diets with different fats (tallow, olive, sunflower, and linseed oils) at 10% from 28 to 48 d of age. Among broilers fed diets with added fat, those fed linseed oil had less abdominal fat (in grams and percentage) than those fed tallow ($P < 0.05$). Absorbed fat losses were slightly higher for birds fed linseed oil, and nitrogen efficiency was lower in those fed tallow ($P < 0.05$). However, there were not significant differences in energy deposition among broilers fed diets with added fat. Fatty acid balance showed the highest values of fatty acid oxidation during the experimental period in broilers fed linseed oil (48.2 g), followed by those fed sunflower oil (23.2 g). Contribution of endogenous fat synthesis to total body fat deposition was minimal in birds fed diets with added fat accounting for 3, 1.2, 8.5, and 7.5 g for broilers fed tallow, olive, sunflower, and linseed oils, respectively. This reflects lipogenesis inhibition by dietary fat addition. Interestingly, between broilers fed diets with added fat, higher values of fatty acids from endogenous synthesis were found in broilers fed diets rich in polyunsaturated fatty acids (PUFA). Results suggest that reduction of abdominal fat in broilers fed linseed oil seems to be a consequence of higher lipid oxidation despite the higher synthesis of endogenous fatty acids.

(*Key words*: broiler, dietary fatty acid profile, energetic balance, fatty acid balance)

2002 Poultry Science 81:1533–1542

INTRODUCTION

Several studies suggest that in both birds and mammals, polyunsaturated fatty acids (PUFA) inhibit lipid synthesis (Wilson et al., 1986,1990; Blake and Clarke, 1990; Ntambi, 1991; Sanz et al., 2000b) and increase fatty acid oxidation (Shimomura et al., 1990; Madsen et al., 1999; Sanz et al., 2000b; Cunnane and Anderson, 1997) and diet-induced thermogenesis (Takeuchi et al., 1995). These effects could explain why PUFA reduce abdominal fat (Crespo and Esteve-Garcia, 2001), fat in other fat depots (Crespo and Esteve-Garcia, 2002) and, consequently, total body fat (Sanz et al., 2000a) when compared to saturated or monounsaturated fats.

Several mechanisms seem to be involved in lower energetic efficiency of PUFA in mammals. Preferential oxidation of PUFA in peroxisomes prior to their oxidation in mitochondria leads to higher energy losses (Clarke, 2000). Furthermore, PUFA are involved in the induction of uncoupling proteins (UCP) in the mitochondria. UCP-3 is restricted to skeletal muscle in rats and is increased twofold by fish oil (Baillie et al., 1999). These mechanisms would reduce the retention of dietary energy in animals fed PUFA with respect to those fed diets rich in saturated fatty acids (SFA). This energy could be dissipated or could be used to enhance protein deposition, as has been suggested by other authors (Sanz et al., 2000a). Different uses of dietary energy for fat and protein depositions or dissipation could be determined by performing a nutrient balance.

The aim of this study was to determine the effect of different dietary fatty acid profiles on nutrient and fatty acid balance in broiler chickens. Lower energetic efficiency of PUFA was expected to decrease energy deposition and to be reflected in fatty acid balance. Effect of different dietary fatty acids on nitrogen and fat retention was also studied to determine different use of dietary energy.

MATERIALS AND METHODS

Animals and Diets

Experimental diets were formulated according to the same criterion as previously described by Crespo and

Received for publication October 19, 2001.
Accepted for publication May 10, 2002.
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Abbreviation Key: MUFA = monounsaturated fatty acids; PPAR = peroxisomal proliferator-activated receptor; PUFA = polyunsaturated fatty acids; SFA = Saturated fatty acids; UCP = uncoupling proteins.

TABLE 1. Fatty acid composition of oils and experimental diets (g/100 g fat)[1]

	Fats and oils				Experimental diets[2]				
Fatty acid[3]	Tallow	Olive oil	Sunflower oil	Linseed oil	B	T	OO	SO	LO
C14:0	3.28	0.00	0.13	0.10	0.20	2.94	0.14	0.13	0.11
C15:0	0.49	0.00	0.00	0.06	0.11	0.45	0.06	0.05	0.03
C16:0	27.2	12.7	6.82	5.93	13.9	24.7	13.9	8.05	7.25
C16:1	2.66	0.98	0.13	0.04	0.20	2.45	0.92	0.13	0.12
C18:0	21.4	2.82	4.48	3.99	2.71	14.8	2.84	3.46	3.30
Trans C18:1 n-9	4.21	0.00	0.00	0.00	0.00	3.13	0.00	0.00	0.00
C18:1 n-9	33.5	69.6	25.0	17.9	17.7	30.6	58.4	21.9	16.9
C18:1 n-7	1.77	2.53	0.60	0.71	0.94	1.64	2.25	0.68	0.78
C18:2 n-6	4.23	9.64	62.2	14.7	57.9	16.9	19.1	64.1	22.0
C18:3 n-6	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C20:0	0.22	0.45	0.32	0.19	0.23	0.19	0.35	0.24	0.34
C18:3 n-3	0.49	0.82	0.09	55.44	5.64	1.73	1.74	1.08	48.78
C20:1 n-9	0.30	0.30	0.17	0.20	0.38	0.31	0.30	0.19	0.22
SFA	52.6	16.0	11.7	10.3	17.2	43.1	17.3	11.9	11.0
UFA	47.4	84.0	88.3	89.7	82.8	56.9	82.7	88.1	89.0
MUFA	42.5	73.4	25.9	18.9	19.2	38.1	61.8	22.8	18.0
PUFA	4.9	10.6	62.4	70.9	63.6	18.8	20.9	65.2	71.0
n-9	38.1	69.9	25.1	18.1	18.1	34.1	58.7	22.0	17.1
n-6	4.4	9.8	62.3	14.8	57.9	17.1	19.1	64.1	22.1
n-3	0.51	0.82	0.09	56.10	5.64	1.73	1.74	1.08	48.9
n-6:n-3	8.69	11.9	672	0.26	10.3	9.89	11.0	59.2	0.45
SFA:UFA	1.11	0.19	0.13	0.11	0.21	0.76	0.21	0.14	0.12

[1]Values are mean of two determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% of added tallow; OO = diet with 10% of added olive oil; SO = diet with 10% of added sunflower oil; LO = diet with 10% of added linseed oil.

[3]SFA = saturated fatty acids; UFA = unsaturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.

Esteve-Garcia (2001). Four diets with four types of added fat (tallow, olive, sunflower, and linseed oils), representing different profiles of fatty acids [SFA, monounsaturated fatty acids (MUFA), and PUFA from n-6 and n-3 series] were used to conduct this experiment. Calculated metabolizable energy was 3,300 kcal/kg. An additional diet without supplemental fat (basal diet) and consequently with lower energy content (2,826 kcal/kg) was also used. Fatty acid profile of experimental diets is shown in Table 1.

One hundred 1-d-old female broiler chickens of the Ross 308 strain were obtained from a commercial hatchery. They were placed in floor pens and fed a commercial starter diet with lard as a fat source. Nutrient balance measurement was performed during the last 20 d before slaughtering on Day 48. In order to avoid effect of experimental diets from Days 21 to 28, birds were fed a diet based on wheat and soybean meal without additional fat during this period of time. On Day 28 of the experiment, 48 birds were weighed and distributed by weight in eight groups, with six birds in each group. One animal of each group was killed by cervical dislocation and stored at –20 C until analysis (a total of eight birds). The remaining 40 chickens were distributed to the treatments with one bird of the same weight group for each treatment (a total of eight birds per treatment belonging to each weight group, which were considered as blocking variable). Two additional chickens per treatment were selected from the rest of the birds to ensure a minimum of eight and maximum of 10 replicates per treatment. Birds were placed in individual cages and fed the experimental diets until Day 48. Feed and water were provided for ad libitum consumption. Feed intake during the experimental period was recorded. From Days 28 to 48, whole droppings were collected daily from each bird, and were stored at –20 C. At the end of the experimental period, whole frozen dropping samples from each chicken were weighed and homogenized in a blade cutter for 2 min. A representative sample from each bird was taken, freeze-dried, and reground for analysis. On Day 48, birds were fasted for 12 h, weighed, and killed by cervical dislocation. After abdominal fat was determined, each whole bird was stored at –20 C and then cut into several pieces and minced in a blade cutter[2] for 5 min. The whole sample was refrozen, freeze-dried, and reground. A representative sample was taken from each animal for later analysis. Broilers killed initially were also minced and freeze-dried in the same way. The animal facilities, working protocol, and killing methods were approved by the IRTA (Institute de Recerca i Tecnologia Agroalimentàries) Ethical Committee.

Analytical Determinations

Dry matter, ash content, moisture, and crude protein of all collected samples were determined as outlined by AOAC (1990). Lipid content was determined by the Folch method (Folch et al., 1957), and gross energy was determined using an adiabatic calorimetric bomb.[3] Car-

[2]Blade cutter: Model CRI-20. Castellvall, Barcelona, Spain.

[3]IKA-Kalorimetersystem C4000 A Adiabatisch. IKA-Analysentechnik GmbH. Heitersheim, Germany.

cass fat (whole body fat, including viscera, skin, and feathers) was determined by subtracting lipid content of abdominal fat (including fat surrounding gizzard, bursa of Fabricius, cloaca, and adjacent muscles) from total body fat. Lipid percentage of abdominal fat pad was assumed to be 87.9% and equal for all treatments, as previously determined (Crespo and Esteve-Garcia, 2001). Fatty acid profile of diets, broilers, and feces was determined as previously reported (Crespo and Esteve-Garcia, 2001). Analytical results of initial broilers were used to estimate the initial body composition of experimental birds. Balance of energy and body components (protein, fat, and fatty acids) were analyzed as follows. Absorbed nutrients and fatty acids were estimated as the difference between ingested and excreted values. Gained nutrients were estimated as the difference between final and initial body composition. Nutrient losses were estimated as the difference between absorbed and gained values. Nutrient efficiency was calculated as percentage of gained nutrients with respect to absorbed nutrients. In the case of the energy balance, absorbed energy corresponded to AME. Energy cost of protein gain was calculated taking a calorimetric value of 5.9 kcal/g of protein (Sibbald and Wolynetz, 1985) and assuming a cost of 1.25 kcal per 1 kcal of protein storage (Pullar and Webster, 1977). Energy cost for fat deposition was assumed to be 0.36 kcal/kcal for birds fed the diet without supplemental fat and 0.16 kcal/kcal for birds fed diets with added fat (Pullar and Webster, 1977; Rothwell et al., 1985). Heat losses were calculated by subtracting energy cost of protein and fat gain from total energy losses (Iossa et al., 2000).

AN = IN − EN.
GN = FBC − IBC.
NL = AN − GN.
NE (%) = (GN × 100) / AN.
EC protein = GN protein (kcal) × 1.25 kcal.
EC fat for basal diet = GN fat (kcal) × 0.36 kcal.
EC fat for diets with fat = GN fat (kcal) × 0.16 kcal.
HL = NL energy − (EC protein + EC fat).

where AN = absorbed nutrients or energy, IN = ingested nutrients or energy, EN = excreted nutrients or energy, GN = gained nutrients or energy, FBC = final body composition, IBC = initial body composition, NL = nutrient or energy losses, NE = nutrient or energy efficiency, and EC = energy cost of deposition. For nitrogen balance, absorbed nitrogen was assumed to be equivalent to gained nitrogen, and nitrogen efficiency was determined as percentage of gained nitrogen with respect to nitrogen intake.

Statistical Analysis

All values were subjected to one-way ANOVA by using the General Linear Model procedure of SAS (SAS Institute, 1992). Body weight group was added to the model as a block factor to avoid variability in body composition due to differences in initial body weight. Final body weight was included as a covariable when needed. When the F-test for treatments was significant at $P < 0.05$ in the ANOVA table, means were compared for significant differences using Duncan's multiple-range test of the same statistical package. In the case of fatty acid balance, percentage of retained saturated and n-9 fatty acids in animals fed the basal diet showed very different standard deviation with respect to those fed the diets with added fat. This was probably due to the amount of endogenous synthesis of these fatty acid families in these birds. Since the main purpose of this experiment was to compare treatments with added fat rather than to compare them with the low-fat diet, percentage of retained SFA and n-9 fatty acids from basal treatment were excluded from the statistical analysis.

RESULTS AND DISCUSSION

Performance parameters were discussed in Crespo and Esteve-Garcia (2002). Body composition and abdominal fat pad values of birds are shown in Table 2. Total gross energy and percentage of body and carcass fat were not significantly affected by treatments. Protein content was lower for birds fed tallow, although differences were only significant for total body protein content in grams. Percentage of protein and ash were higher for birds fed the basal diet ($P < 0.05$) due to the lower body weight of these birds. Thus, differences in body weight of broilers fed the basal diet with respect to those fed the diets with added fat were due to lower body fat and moisture contents. Total protein deposition was similar to the rest of the treatments, suggesting that the energy content of the diet did not limit protein deposition.

Birds fed sunflower and linseed oils showed less abdominal fat than those fed tallow or olive oil, although statistical differences were only found between broilers fed tallow and those fed linseed oil. This is in agreement with other experiments in which abdominal fat was reduced with polyunsaturated fatty acids with respect to saturated or monounsaturated fatty acids (Sanz et al., 1999; Crespo and Esteve-Garcia, 2001). However, in this experiment differences in abdominal fat were not as great in absolute values as those found in Crespo and Esteve-Garcia (2001). These different results could be due to the greater body weight of birds in the previous experiment, because percentage of reduction was similar in both experiments.

Birds fed tallow showed higher gross energy intake than the rest of treatments (Table 3). This was counteracted by higher fecal energy losses, resulting in an equal intake of AME for all treatments. Thus, percentage of AME was lower for the diets with added tallow, although differences were not significant. Although not significant, our results tend to follow results obtained by other authors (Fuller and Rendon, 1977; Allen et al., 1997; Dvorin et al., 1998) who found lower digestibility and lower ME of diets with higher SFA content with respect to those with higher percentages of PUFA. Total

TABLE 2. Body composition and abdominal fat[1]

Item[2]	Final BW (g)	GE[3] (cal/g)	Body fat (%)	Body fat (g)	Carcass fat[4] (%)	Carcass fat[4] (g)	Crude protein (%)	Crude protein (g)	Ash (%)	Ash (g)	Moisture (%)	Moisture (g)	Abdominal fat (%)	Abdominal fat (g)
B	2,111^{b}	1,969	11.1	234	10.0	210^{b}	20.5^{a}	433^{a}	2.42^{a}	51.1^{ab}	66.2	1,396^{d}	1.35^{d}	28.3^{c}
T	2,224^{a}	2,142	13.2	293	11.4	253^{a}	18.7^{b}	416^{b}	2.17^{b}	48.4^{bc}	65.6	1,460^{c}	2.09^{a}	47.0^{a}
OO	2,271^{a}	2,118	12.7	290	11.0	252^{a}	19.1^{b}	432^{a}	2.09^{b}	47.2^{c}	66.0	1,497^{ab}	1.89^{ab}	43.1^{ab}
SO	2,301^{a}	2,094	12.9	298	11.3	260^{a}	18.8^{b}	432^{a}	2.26^{b}	52.0^{a}	65.9	1,514^{a}	1.77^{abc}	41.3^{ab}
LO	2,227^{a}	2,126	12.5	277	11.0	245^{a}	18.9^{b}	421^{ab}	2.09^{b}	46.5^{c}	66.0	1,469^{bc}	1.64^{bc}	36.2^{bc}
Root MS error	123.9	154.5	1.62	37.9	1.34	31.5	0.62	13.7	0.163	3.47	1.53	35.6	0.456	10.34

[a-c]Values in the same column with no common superscript differ significantly.

[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% of added tallow; OO = diet with 10% of added olive oil; SO = diet with 10% of added sunflower oil; LO = diet with 10% of added linseed oil.

[3]GE = gross energy.

[4]Carcass fat = total body fat without abdominal fat.

energy gain and energy losses did not statistically differ between treatments, although birds fed the basal diet showed lower energy gain and higher energy losses per 100 g of weight gain with respect to those fed diets with added fat, leading to a lower energetic efficiency. Although these values were not statistically significant, other authors have found lower energetic efficiency of diets without added fat with respect to those with added fat (Carew et al., 1964; Fuller and Rendon, 1977;1979; Nitsan et al., 1997). This could be the consequence of the higher energy cost of protein and fat gain. Higher protein gain per 100 g of weight gain and endogenous synthesis of fatty acid resulted in higher energy cost with respect to broilers fed diets with added fat in which percentage of protein gain was lower, and fat gain was due mainly to direct deposition from dietary fat. Consequently, energy losses as heat production with respect to total energy losses were lower ($P < 0.05$) in birds fed the basal diet compared to those fed the high fat diets. This suggests that increasing dietary fat inclusion produces higher derivation of energy to heat production that, in turn, causes worse efficiency of fat deposition. The same effect was also found in previous experiments in rats (Iossa et al., 2000). In our case, other factors could be implicated, such as different body weight between broilers fed the basal diet and the diets with added fat. There were no significant differences in energy gain, energetic efficiency, and energy losses between broilers fed diets with added fat. Different results were found in the experiment of Brue and Latshaw (1985), in which broilers fed diets with tallow showed higher ME intake, higher energetic efficiency, and higher energy deposition compared to those fed corn oil (rich in PUFA).

Broilers fed the basal diet ingested the lowest amount of fat and had the lowest fat digestibility ($P < 0.05$) (Table 4) as also found by Fuller and Rendon (1979) and Nitsan et al. (1997). However, these birds showed negative values of fat losses and a percentage of fat efficiency much higher than 100%, indicating higher endogenous fat synthesis than broilers fed diets with added fat ($P < 0.05$), in agreement with previous reports (Donaldson, 1985; Rosebrough et al., 1999). Birds fed tallow showed higher

TABLE 3. Energy balance per 100 g of weight gain (kcal)[1]

Item[2]	GE[3] intake	Excreted (GE	AME	AME (%)	Energy gain[4]	Total energy losses[5]	Energy efficiency[6] (%)	Energy cost of protein gain[7]	Energy cost of fat gain[8]	Heat losses[9] (%)
B	874^{b}	307^{b}	567	65.1	216	351	38.0	161^{a}	31.1^{a}	45.0^{b}
T	972^{a}	386^{a}	586	60.4	243	343	41.4	139^{b}	21.1^{b}	53.3^{a}
OO	863^{b}	301^{b}	563	65.5	238	324	42.2	142^{b}	19.9^{b}	49.8^{a}
SO	884^{b}	313^{b}	571	65.2	234	338	40.8	140^{b}	19.5^{b}	52.6^{a}
LO	903^{ab}	322^{b}	582	64.6	242	340	41.7	141^{b}	20.7^{b}	52.0^{a}
Root MS error	70.6	62.3	23.8	4.47	25.6	20.5	3.54	7.0	4.63	3.88

[a,b]Values in the same column with no common superscript differ significantly.

[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% of added tallow; OO = diet with 10% of added olive oil; SO = diet with 10% of added sunflower oil; LO = diet with 10% of added linseed oil.

[3]GE = gross energy.

[4]Energy gain = final body energy − initial body energy.

[5]Total energy losses = AME − energy gain.

[6]Energy gain with respect to AME intake.

[7]Energy cost of protein gain = kilocalories of protein gain × 1.25 kcal.

[8]Energy cost of fat gain = kilocalories of fat gain × 0.36 kcal for basal diet and 0.16 kcal for diets with added fat.

[9]Heat losses = total E losses − energy cost of protein and fat deposition. Percentage calculated with respect to total E losses and includes maintenance requirements and heat increment.

TABLE 4. Fat balance per 100 g of weight gain (g)[1]

Item[2]	Fat intake	Excreted fat	Digested fat	Digestibility (%)	Fat gain	Fat losses	Efficiency[3] (%)
B	7.50[d]	3.15[b]	4.35[b]	58.4[b]	12.5	–8.16[b]	293[a]
T	26.0[a]	9.35[a]	16.6[a]	64.2[ab]	15.9	0.71[a]	95.6[b]
OO	22.2[c]	6.62[a]	15.6[a]	70.8[a]	15.0	0.66[a]	95.1[b]
SO	23.0[bc]	7.30[a]	15.7[a]	69.3[a]	15.3	0.32[a]	97.8[b]
LO	24.3[b]	7.60[a]	16.7[a]	68.7[a]	14.9	1.75[a]	89.6[b]
Root MS error	1.70	2.589	1.69	9.97	2.68	2.115	29.61

[a-c]Values in the same column with no common superscript differ signficantly.

[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% added tallow; OO = diet with 10% added olive oil; SO = diet with 10% added sunflower oil; LO = diet wiht 10% added linseed oil.

[3]Fat gain with respect to digested fat.

fat intake ($P < 0.05$) and higher fecal fat losses leading to the same absorbed fat and to lower digestibility ($P = 0.09$) compared to the rest of diets with added fat. Similar results were found by Dvorin et al. (1998) with diets with a high level of SFA. Fat gain per 100 g of weight gain was slightly lower for broilers fed linseed oil with respect to the other treatments with added fat, and this was concomitant with higher fat losses and lower percentage of fat efficiency. However, these differences were not significant. Since protein gain was similar within treatments with added fat (Table 5), this low fat accretion in broilers fed linseed oil should have been reflected in energy accretion. However, due to small differences or to high individual variations, this slight effect in fat balance might have not been detected in energy balance. However, this effect was observed by Sanz et al. (2000a) who obtained lower energy gain and higher heat losses in broilers fed sunflower oil compared to those fed a blend of lard and tallow.

Broilers fed the basal diet or tallow ingested a higher amount of dietary nitrogen than the rest of treatments ($P < 0.05$). However, only broilers fed the basal diet showed higher nitrogen gain per 100 g of weight gain ($P < 0.05$), leading to higher efficiency of nitrogen deposition compared to broilers fed tallow. Thus, although birds fed the tallow diet ingested more nitrogen than the rest of the treatments with added fat, they did not increase nitrogen gain compared to broilers fed olive, sunflower, or linseed oils, leading to lower nitrogen efficiency with respect to birds fed the basal diet or diets with added olive or sunflower oil ($P < 0.05$). Thus, increasing ingestion of nitrogen over required levels produced a decrease in nitrogen retention efficiency as previously reported by Geraert et al. (1990).

TABLE 5. Nitrogen balance per 100 g weight gain (g)[1]

Item[2]	N intake	Excreted N	N gain	N efficiency[3] (%)
B	7.58[a]	4.10[ab]	3.50[a]	46.4[a]
T	7.56[a]	4.22[a]	3.01[b]	40.1[b]
OO	6.75[b]	3.40[c]	3.08[b]	46.0[a]
SO	6.92[b]	3.52[bc]	3.03[b]	44.5[a]
LO	7.07[ab]	3.65[abc]	3.06[b]	43.6[ab]
Root MS error	0.564	0.617	0.152	4.19

[a-c]Values in the same column with no common superscript differ significantly.[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% added tallow; OO = diet with 10% of added olive oil; SO = diet with 10% of added sunflower oil; LO = diet with 10% of added linseed oil.

[3]N gain with respect to N intake.

Fatty acid balance is shown in Table 6. Birds fed tallow ingested the highest amount of SFA. However, digestibility of SFA in these birds was lower than that of birds fed olive oil ($P < 0.05$) and slightly lower than that of birds fed sunflower or linseed oil. This suggests an improvement of SFA digestibility when vegetable oils with higher levels of unsaturated fatty acids are included in the diet (Sibbald and Kramer, 1980). SFA gain was higher in broilers fed the tallow diet, due to higher ingestion. However, percentage of saturated fatty acid gain with respect to absorbed fatty acids was lower for these birds. High fatty acid oxidation is related to PUFA and not to SFA. Therefore, this disappearance of SFA in broilers fed tallow is probably due, in part, to elongation and desaturation processes leading to the formation of MUFA. In fact, boilers fed tallow presented negative values of n-9 fatty acid oxidation that could be due to de novo endogenous synthesis or to elongation and desaturation of SFA. In the rest of the treatments, percentage of retained SFA reached values above 100%, suggesting endogenous synthesis of these fatty acids, which was much higher in broilers fed the basal diet. Within treatments with added fat, broilers fed sunflower and linseed oil showed similar values of net endogenous synthesis accounting to 8.5 and 7.4 g (negative oxidation values), respectively. These values were only different from those in broilers fed tallow and those fed the basal diet ($P < 0.05$).

Ingestion of n-9 fatty acids was higher for broilers fed olive oil. Digestibility of these fatty acids was equal between broilers fed diets with added fat. Only broilers fed olive oil presented higher digestibility of n-9 fatty acids compared to those fed the basal diet ($P < 0.05$). N-9 fatty acid gain was higher for birds fed olive oil, followed by broilers fed tallow. The lowest gain was for broilers fed sunflower and linseed oils due to their lower ingestion. Percentage of gained n-9 was similar for all treatments with added fat, although, as for SFA, broilers

TABLE 6. Fatty acid balance[1,2]

Item	B	T	OO	SO	LO	Root MS error
	Saturated fatty acids					
Initial (g)[3]	20.7	20.7	20.8	20.8	21.3	1.72
Final (g)[3]	66.6^{b}	81.9^{a}	57.5^{bc}	51.0^{c}	48.7^{c}	11.23
Ingested (g)	14.0^{d}	130.0^{a}	47.4^{b}	34.3^{c}	31.2^{c}	6.59
Excreted (g)	6.10^{c}	49.7^{a}	12.9^{b}	14.0^{b}	11.2^{bc}	5.740
Absorbed (g)	7.92^{d}	80.3^{a}	34.5^{b}	20.3^{c}	20.0^{c}	5.410
Digestibility (%)	57.3^{b}	61.8^{b}	73.5^{a}	64.6^{ab}	63.9^{ab}	9.36
Gained (g)[3]	45.9^{b}	61.0^{a}	36.5^{bc}	30.2^{c}	27.4^{c}	10.71
Gained (%)[4]	611	74.6^{b}	102^{b}	140^{a}	141^{a}	33.11
Oxidation (g)	–38.0	19.9^{a}	–1.20^{b}	–8.49^{b}	–7.38^{b}	8.934
	n-9 fatty acids					
Initial (g)	30.4	30.4	30.5	30.6	31.3	2.52
Final (g)	75.0^{c}	107^{b}	143^{a}	68.8^{c}	63.9^{c}	21.82
Ingested (g)	14.8^{e}	103^{b}	161^{a}	63.3^{c}	48.5^{d}	13.54
Excreted (g)	5.06^{d}	29.7^{ab}	38.1^{a}	19.8^{bc}	13.9^{cd}	13.637
Absorbed (g)	9.70^{d}	73.1^{b}	123^{a}	43.6^{c}	34.6^{c}	12.688
Digestibility (%)	66.0^{b}	70.9^{ab}	76.9^{a}	73.3^{ab}	71.3^{ab}	9.06
Gained (g)	44.6^{c}	75.9^{b}	112^{a}	38.1^{c}	32.6^{c}	20.61
Gained (%)[4]	456	106	87.0	82.6	94.2	22.74
Oxidation (g)	–34.9^{c}	–3.01^{b}	13.8^{a}	7.26^{ab}	1.98^{ab}	13.214
	n-6 fatty acids					
Initial (g)	12.9	13.0	13.0	13.0	13.3	1.07
Final (g)	43.7^{b}	40.9^{b}	46.0^{b}	140^{a}	44.7^{b}	12.78
Ingested (g)	47.3^{c}	51.5^{bc}	52.4^{bc}	184^{a}	62.5^{b}	12.46
Excreted (g)	14.4^{b}	16.1^{b}	16.4^{b}	41.3^{a}	18.4	11.39
Absorbed (g)	32.9^{c}	35.4^{c}	36.0^{c}	143	44.1^{b}	6.30
Digestibility (%)	70.0^{b}	68.7^{b}	69.3^{b}	79.4^{a}	70.7^{b}	7.24
Gained (g)	30.8^{b}	27.8^{b}	32.9^{b}	127^{a}	31.3^{b}	12.35
Gained (%)	93.5^{a}	78.4^{ab}	87.2^{a}	88.3^{a}	71.0^{b}	13.77
Oxidation (g)	2.13^{c}	7.68^{bc}	3.98^{c}	15.9^{a}	12.8^{ab}	7.315
	n-3 fatty acids					
Initial (g)	1.37	1.37	1.37	1.38	1.41	0.114
Final (g)	3.93^{b}	5.41^{b}	4.58^{b}	3.11^{a}	80.8^{a}	4.954
Ingested (g)	4.60^{b}	5.21^{b}	4.76^{b}	3.11^{b}	138^{a}	5.241
Excreted (g)	1.24^{b}	1.44^{b}	1.39^{b}	1.04^{b}	25.6^{a}	4.704
Absorbed (g)	3.36^{b}	3.77^{b}	3.37^{b}	2.07^{b}	113^{a}	4.132
Digestibility (%)	73.2^{b}	72.3^{b}	71.4^{b}	66.4^{b}	81.8^{a}	7.05
Gained (g)[5]	2.56^{b}	4.03^{b}	3.19^{b}	1.73^{b}	79.4^{a}	4.907
Gained (%)	75.8^{bc}	107^{a}	90.9^{ab}	84.8^{bc}	70.4^{c}	18.128
Oxidation (g)[5]	0.81^{b}	–0.25^{b}	0.26^{b}	0.29^{b}	33.4^{a}	3.795

[a-d]Values in the same row of the same group of fatty acids with no common superscript differ signficantly.

[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% added tallow; OO = diet with 10% added olive oil; SO = diet with 10% added sunflower oil; LO = diet with 10% added linseed oil.

[3]Initial = fatty acid content of broilers at the beginning of the experimental period; Final = fatty acid content of broilers at the end of the experimental period; Gained (g) = difference between intital and final composition; Gained (%) = percentage of gained respect to absorbed.

[4]Values of basal diet are excluded from the statistical analysis.

[5]Values of basal, tallow, olive, and sunflower oil diets were not statistically different from zero.

fed the diet with no supplemental fat presented the highest values of percentage of n-9 fatty acid gain and the lowest values of oxidation. Between broilers fed the diets with supplemental fat, those fed olive oil showed the highest values of n-9 fatty acid oxidation, although differences were only significant with respect to birds fed tallow. Broilers fed tallow presented negative values of fatty acid oxidation suggesting some endogenous synthesis or derivation from SFA.

From the total sum of negative oxidation values of saturated, n-9, and n-7 fatty acids (data not shown), we can deduce that net endogenous fat synthesis in broilers fed diets with supplemental fat represents a low percentage of the total fat deposition. This sum accounts to 8.4, 3.3, 10.8, and 10.2 g for broilers fed tallow, olive, sunflower, and linseed oils, respectively. Similar or slightly higher values for broilers fed sunflower and linseed oils compared to those fed tallow suggest similar or slightly higher net endogenous fat synthesis in birds fed diets rich in PUFA, which is in disagreement with studies showing inhibition of lipid synthesis by PUFA (Wilson et al., 1986; Blake and Clarke, 1990; Wilson et al., 1990; Ntambi, 1991; Sanz et al., 2000b).

Broilers fed sunflower oil ingested the highest amount and presented the highest digestibility of n-6 fatty acids. Percentage of n-6 fatty acid gain was lower for broilers fed linseed oil than for the rest of the treatments. This was due to the high oxidation of n-6 fatty acids that

TABLE 7. Total body fatty acid (% of deposited fat)[1,2]

Fatty acid[3]	B	T	OO	SO	LO	Root MS error
C14:0	0.72^{b}	2.48^{a}	0.26^{c}	0.28^{c}	0.31^{c}	0.141
C15:0	0.11^{b}	0.36^{a}	0.11^{b}	0.04^{b}	0.09^{b}	0.080
C16:0	25.9^{a}	23.1^{a}	17.0^{b}	10.7^{c}	10.9^{c}	4.53
C16:1n-7	7.41^{a}	5.42^{b}	1.99^{c}	0.67^{d}	1.06^{cd}	1.199
C18:0	6.86^{ab}	8.28^{a}	4.77^{bc}	4.12^{c}	4.52^{bc}	2.328
Trans C18:1 n-9	0.00^{b}	1.39^{a}	0.00^{b}	0.00^{b}	0.00^{b}	0.154
C18:1 n-9	31.8^{c}	39.4^{b}	55.2^{a}	18.6^{d}	18.2^{d}	5.19
C18:1 n-7	2.27^{a}	2.34^{a}	2.10^{a}	0.49^{b}	0.77^{b}	0.361
C18:2 n-6	20.0^{b}	13.6^{d}	14.9^{cd}	61.9^{a}	17.8^{bc}	2.94
C18:3 n-6	0.52^{a}	0.16^{bc}	0.17^{bc}	0.35^{ab}	0.05^{c}	0.245
C20:0	0.09^{b}	0.12^{b}	0.13^{b}	0.00^{c}	0.31^{a}	0.062
C18:3 n-3	1.47^{b}	1.39^{b}	1.22^{b}	0.99^{b}	43.0^{a}	0.933
C20:1 n-9	0.29^{a}	0.05^{c}	0.35^{a}	0.06^{c}	0.18^{b}	0.063
C20:2 n-6	0.21^{b}	0.13^{c}	0.12^{c}	0.47^{a}	0.13^{c}	0.068
C20:3 n-3	0.00^{b}	0.00^{b}	0.00^{b}	0.00^{b}	0.50^{a}	0.017
C20:4 n-6	0.98^{a}	0.73^{b}	0.66^{b}	0.91^{a}	0.10^{c}	0.130
C20:5 n-3	0.07^{b}	0.04^{b}	0.04^{b}	0.00^{b}	1.19^{a}	0.093
C22:4 n-6	0.96^{a}	0.37^{ab}	0.60^{a}	0.67^{a}	0.00^{b}	0.560
C22:5 n-3	0.22^{c}	0.47^{b}	0.19^{c}	0.00^{d}	0.78^{a}	0.223
C22:6 n-3	0.11^{c}	0.27^{b}	0.16^{c}	0.18^{c}	0.38^{a}	0.092
SFA	33.7^{a}	34.3^{a}	22.3^{b}	15.1^{c}	16.1^{bc}	6.64
UFA	66.3^{c}	65.7^{c}	77.7^{b}	84.9^{a}	83.9^{ab}	6.64
MUFA	41.8^{c}	48.6^{c}	59.6^{a}	19.8^{d}	20.2^{d}	6.14
PUFA	24.5^{b}	17.1^{c}	18.1^{c}	65.1^{a}	63.7^{a}	3.13
n-9	32.1^{c}	40.8^{b}	55.6^{a}	18.6^{d}	18.4^{d}	5.26
n-6	22.7^{b}	15.0^{c}	16.5^{c}	64.3^{a}	17.9^{c}	2.84
n-7	9.68^{a}	7.76^{b}	4.04^{c}	1.17^{d}	1.83^{d}	1.446
n-3	1.87^{bc}	2.17^{b}	1.60^{bc}	0.84^{c}	45.8	1.059
n-9:n-6	1.45^{c}	2.76^{b}	3.38^{a}	0.29^{e}	1.03^{d}	0.280
n-9:n-3	17.8^{c}	18.9^{bc}	35.3^{a}	22.7^{b}	0.40^{d}	4.122
n-6:n-3	12.4^{b}	6.90^{b}	10.5^{b}	81.7^{a}	0.40^{b}	3.90
SFA:UFA	0.51	0.53^{a}	0.32^{b}	0.18^{b}	0.19^{b}	0.156

$^{a-d}$Values in the same row with no common superscript differ significantly.

[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% added tallow; OO = diet with 10% added olive oil; SO = diet with 10% added sunflower oil; LO = diet with 10% added linseed oil.

[3]SFA = saturated fatty acids; UFA = unsaturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.

occurred in these birds ($P < 0.05$). Broilers fed sunflower oil presented similar values of n-6 fatty acid oxidation as the rest of the treatments.

Broilers fed linseed oil presented the highest values of n-3 fatty acid gain, digestibility, and oxidation. However, in the rest of treatments, ingestion of n-3 fatty acids was so low that measured values may not be accurate. In fact, values of n-3 fatty gain and oxidation in birds fed the other treatments are not statistically different from zero. Thus, we could not study n-3 fatty acid behavior in broilers fed diets rich in other families of fatty acids.

Results obtained in this experiment suggest that broilers fed linseed oil tend to oxidize more polyunsaturated fatty acids than those fed the other treatments. Several studies have shown that diets rich in PUFA enhance lipid oxidation (Shimomura et al., 1990; Madsen et al., 1999; Sanz et al., 2000b; Cunnane and Anderson, 1997) and this oxidation is higher for PUFA than for saturated fatty acids (Leyton et al., 1987). These effects seem to be mediated at the level of gene transcription regulation of enzymes involved in lipid oxidation (Brandt et al., 1998; Clarke, 2000; Clarke, 2001). Binding of PUFA to the peroxisomal proliferator-activated receptor (PPAR) leads to the induction of several hepatic, cardiac and skeletal muscle genes encoding proteins involved in lipid transport, peroxisomal oxidation, and thermogenesis. Moreover, PUFA (and mainly those from n-3 series) seem to enhance thermogenesis by inducing mitochondrial UCP (Baillie et al., 1999).

Results in this experiment show more PUFA oxidation in birds fed linseed oil compared to those fed tallow or olive oil. However, broilers fed sunflower oil did not show the same effect as those fed linseed oil. This is in disagreement with results obtained by other investigators (Sanz et al., 2000b; Shimomura et al., 1990). However, Fu and Sinclair (2000) suggested that guinea pigs fed diets with linolenic and linoleic acids tend to oxidize linolenic acid in a higher proportion than linoleic acid while the latter tends to be deposited in tissues. Furthermore, biochemical studies suggest different mechanisms of action of n-3 and n-6 fatty acids. Different isoforms of PPAR seem to have different actions in lipid metabolism, and n-3 and n-6 fatty acids activate these PPAR isoforms with different potency. Thus, PPARα is related to the induction of peroxisomal enzymes, which are more strongly activated by n-3 than by n-6 fatty acids (Power and Newsholme, 1997). On the other hand, PPARγ plays roles in

TABLE 8. Total body fatty acid (g/100 g fat)[1,2]

Fatty acid[3]	B	T	OO	SO	LO	Root MS error
C14:0	0.77[b]	2.01[a]	0.44[c]	0.44[c]	0.39[c]	0.083
C15:0	0.12[b]	0.29[a]	0.11[bc]	0.07[c]	0.08[bc]	0.047
C16:0	24.3[a]	22.6[a]	18.2[b]	13.6[c]	11.9[c]	3.11
C16:1 n-7	7.46[a]	6.02[b]	3.66[c]	2.56[d]	2.78[d]	0.748
C18:0	6.54[ab]	7.62[a]	5.05[bc]	4.60[c]	3.66[c]	1.599
Trans C18:1 n-9	0.00[b]	1.00[a]	0.00[b]	0.00[b]	0.00[b]	0.104
C18:1 n-9	35.1[c]	39.9[b]	51.1[a]	24.9[d]	22.2[d]	3.50
C18:1 n-7	2.50[a]	2.50[a]	2.31[a]	1.17[b]	1.23[b]	0.231
C18:2 n-6	18.6[b]	14.3[c]	15.4[c]	49.2[a]	18.6[b]	1.82
C18:3 n-6	0.43[a]	0.18[bc]	0.19[bc]	0.32[ab]	0.11[c]	0.170
C20:0	0.12[b]	0.13[b]	0.14[b]	0.03[c]	0.26[a]	0.041
C18:3 n-3	1.29[b]	1.26[b]	1.14[b]	0.98[b]	35.28[a]	0.658
C20:1 n-9	0.36[a]	0.17[c]	0.40[a]	0.18[c]	0.24[b]	0.043
C20:2 n-6	0.19[b]	0.14[c]	0.14[c]	0.38[a]	0.16[bc]	0.048
C20:3 n-3	0.00[b]	0.00[b]	0.00[b]	0.00[b]	0.38[a]	0.014
C20:4 n-6	0.87[a]	0.71[a]	0.66[a]	0.84[a]	0.36[b]	0.084
C20:5 n-3	0.07[b]	0.05[bc]	0.05[bc]	0.00[c]	1.01[a]	0.063
C22:4 n-6	0.50[a]	0.36[ab]	0.52[a]	0.58[a]	0.07[b]	0.218
C22:5 n-3	0.38[bc]	0.51[b]	0.32[c]	0.03[d]	0.91[a]	0.154
C22:6 n-3	0.14[c]	0.25[b]	0.17[c]	0.18[c]	0.35[a]	0.063
SFA	31.8[a]	32.7[a]	24.0[b]	18.8[c]	19.8[bc]	4.58
UFA	68.2[c]	67.3[c]	76.1[b]	81.2[a]	80.2[ab]	4.58
MUFA	45.4[c]	49.6[b]	57.5[a]	28.8[d]	29.9[d]	4.07
PUFA	22.8[c]	17.8[d]	18.5[d]	52.5[a]	50.3[b]	2.01
n-9	35.5[c]	41.0[b]	51.5[a]	25.0[d]	25.5[d]	3.54
n-6	20.9[b]	15.7[d]	16.9[cd]	51.4[a]	17.9[c]	1.72
n-7	9.96[a]	8.52[b]	5.97[c]	3.73[d]	4.43[d]	0.896
n-3	1.87[bc]	2.08[b]	1.68[bc]	1.13[c]	32.44[a]	0.743
n-9:n-6	1.82[c]	2.75[b]	3.20[a]	0.45[e]	1.45[d]	0.244
n-9:n-3	21.9[b]	21.9[b]	30.8[a]	23.1[b]	0.80[c]	4.62
n-6:n-3	11.5[b]	7.80[b]	9.60[b]	49.6[a]	0.60[c]	4.20
SFA:UFA	0.47[a]	0.49[a]	0.33[b]	0.23[b]	0.25[b]	0.103

[a-d]Values in the same row with no common superscript differ significantly.

[1]Values are means of 10 determinations.

[2]B = basal diet without supplemental fat; T = diet with 10% of added tallow; OO = diet with 10% of added olive oil; SO = diet with 10% of added sunflower oil; LO = diet with 10% of added linseed oil.

[3]SFA = saturated fatty acids; UFA = unsaturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.

fat cell differentiation and expression of lipoprotein lipase, fatty acid binding-protein, and glucose transporter. This isoform seems to be activated more strongly by n-6 fatty acids (Wolf, 1996; Mater et al., 1998). Thus, in this experiment reduction in abdominal fat in broilers fed linseed oil could be explained by higher lipid oxidation and perhaps higher thermogenesis. In broilers fed sunflower oil, the effect of PUFA was not strong enough to produce a significant effect on total body fat deposition in contrast with Sanz et al. (2000a) who found that broilers fed sunflower oil presented lower abdominal and body fat than those fed diets rich in SFA.

Fatty acid composition of deposited body fat is presented in Table 7. Broilers fed the basal diet presented higher percentage of SFA and n-9 fatty acids and lower percentage of n-6 and n-3 fatty acids than that observed with the other diets. This effect was probably due to the endogenous synthesis that took place in these animals. In broilers fed tallow, a reduction in percentage of SFA and an increase in n-9 fatty acids with respect to dietary fat percentage of these fatty acids was observed. This agrees with the higher disappearance of SFA fatty acids in these birds. That the percentage of all SFA had decreased and the main MUFA (C16:1 n-7, C18:1 n-9, and C18:1 n-7) had increased compared to the other diets suggest that disappearance of SFA was due, in part, to its elongation and desaturation to form MUFA. Thus, endogenous synthesis of n-9 fatty acids observed in fatty acid balance (Table 6) could be a consequence of the transformation of SFA to MUFA. In broilers fed olive oil, the percentage of SFA was slightly higher, and percentage of n-9 was slightly lower than that of the diet, in agreement with the negative value of SFA oxidation and positive value of n-9 oxidation observed in the fatty acid balance for these birds and similar to broilers fed sunflower oil. Also, according to results in fatty acid balance, broilers fed linseed oil presented a higher percentage of SFA and lower percentage of n-6 and n-3 fatty acids with respect to the fatty acid profile of dietary fat.

Dietary fatty acid profile was reflected in broilers fed the treatments with added fat as found by other authors (Hulan et al. 1984; Ajuyah et al., 1991) (Table 8). The highest percentage of SFA was found in broilers fed tallow or the basal diet. Whereas C14:0, C15:0, and C18:0 were in higher proportion in broilers fed tallow, C16:0 and C16:1 n-7 presented higher values in broilers fed the basal diet despite their lower presence in the diet, presumably due to endogenous synthesis. In birds fed

olive oil, SFA in body fat were replaced by oleic acid (C18:1 n-9). However, although C18:0 was lower in muscle and abdominal fat of birds fed olive oil than in those fed tallow, sunflower, or linseed oil (Crespo and Esteve-Garcia, 2001), the percentage of C18:0 in total body fat of broilers fed olive oil was similar to that of broilers fed sunflower or linseed oils. This finding suggests that reduction of C18:0 in abdominal, breast, and thigh fat in broilers fed olive oil compared to those fed tallow, sunflower, or linseed oils could be compensated by an increase in the remainder of body fat.

Broilers fed sunflower oil had higher values of linoleic acid (C18:2 n-6) and other n-6 derivatives than those in the treatments. These fatty acids replaced SFA and MUFA with respect to broilers fed tallow. The same effect was observed with n-3 fatty acids in broilers fed linseed oil. Replacement of MUFA by n-3 fatty acids was also found by Ajuyah et al. (1991). Whereas stearic acid remained constant within abdominal, thigh, and breast fat in broilers fed tallow, sunflower, and linseed oil (Crespo and Esteve-Garcia, 2001), this fatty acid decreased in body fat of broilers fed sunflower and linseed oil, with respect to those fed tallow. Thus, stearic acid seemed to act differently depending on the fatty acid profile of the diet.

In diets rich in oleic acid, stearic acid tends to be deposited in carcass fats other than abdominal, breast, and thigh fat, while in diets rich in PUFA, this fatty acid tends to be in higher proportions in abdominal, breast, and thigh fat compared to the rest of the body fat. Despite the higher content of linoleic acid in the diet with linseed oil with respect to those with tallow or olive oil, n-6 derivatives were found in higher amounts in broilers fed tallow or olive oil compared to those fed linseed oil, while linoleic acid was higher in broilers fed linseed oil. This effect reflects the competition for Δ-5 and Δ-6 desaturases between n-3 and n-6 fatty acids. For the same reason, broilers fed sunflower oil had the lowest values of n-3 derivatives.

Results of this experiment suggest that reduction in abdominal fat of broilers fed diets rich in PUFA (mainly of n-3 series) compared to those fed diets rich in SFA or MUFA seems to be due to higher fatty acid oxidation. However, apparent higher endogenous fatty acid synthesis in broilers fed sunflower and linseed oils is in disagreement with other studies that show inhibition of lipogenic enzymes by dietary PUFA. Thus, this effect should be confirmed by in vivo determinations of lipogenesis in broilers fed different dietary fatty acids.

ACKNOWLEDGMENTS

This project has been supported by INIA (Instituto Nacional de Investigación Agraria, of Spanish Government) Project Number SC 97-045 and fellowship 1997 to 2000 and CIRIT (of the Catalonian Government) Quality Research Group Reference Number GRQ93-9804.

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