Diets supplemented with starch and corn oil, marine algae, or hydrogenated palm oil differentially modulate milk fat secretion and composition in cows and goats: A comparative study

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ABSTRACT

A direct comparative study of dairy cows and goats was performed to characterize the animal performance and milk fatty acid (FA) responses to 2 types of diets that induce milk fat depression in cows as well as a diet that increases milk fat content in cows but for which the effects in goats are either absent or unknown. Twelve Holstein cows and 12 Alpine goats, all multiparous, nonpregnant, and at 86 ± 24.9 and 61 ± 1.8 DIM, respectively, were allocated to 1 of 4 groups and fed diets containing no additional lipid (CTL) or diets supplemented with corn oil [5% dry matter intake (DMI)] and wheat starch (COS), marine algae powder (MAP; 1.5% DMI), or hydrogenated palm oil (HPO; 3% DMI), according to a 4×4 Latin square design with 28-d experimental periods. Dietary treatments had no significant effects on milk yield and DMI in both species, except for COS in cows, which decreased DMI by 17%. In cows, milk fat content was lowered by COS (–45%) and MAP (–22%) and increased by HPO (13%) compared with CTL, and in goats only MAP had an effect compared with CTL by decreasing milk fat content by 15%. In both species, COS and MAP lowered the yields (mmol/d per kg of BW) of <C16 and C16 FA. With COS, this decrease was compensated by an increase of >C16 FA in goats, but not in cows, and the >C16 FA yield decreased with MAP in both species. HPO supplementation increased the milk yield of C16 FA in cows. Compared with CTL, COS induced an increase of *trans*-10, *cis*-12 conjugated linoleic acid by 18 fold in cows and 7 fold in goats and of *trans*-10 18:1 by 13 fold in cows and 3 fold in goats. Moreover, other conjugated linoleic acid isomers, such as *trans*-10, *trans*-12 and *trans*-7, *cis*-9, were increased to a greater extent in cows (8 and 4 fold, respectively) compared with goats (4 and 2 fold, respectively) on

the COS treatment. In both species, the responses to MAP were characterized by a decrease in the milk concentration of 18:0 (3 fold, on average) and *cis*-9 18:1 (2 fold, on average) combined with a 3-fold increase in the total *trans* 18:1, with an increase in *trans*-10 18:1 only observed in cows. Compared with CTL, the response to HPO was distinguished by an increase in 16:0 (10%) in cows. This comparative study clearly demonstrated that each ruminant species responds differently to COS and HPO treatments, whereas MAP caused similar effects, and that goats are less sensitive than cows to diets that induce a shift from the *trans*-11 toward the *trans*-10 ruminal pathways.

Key words: ruminant species, lipid supplement, milk fatty acid, milk fat plasticity

INTRODUCTION

The ability to better control milk fat content and composition is central to improving both the nutritional quality of dairy products, as some fatty acids (FA) have potential positive or negative effects on human health (Givens, 2015; Ferlay et al., 2017), and the production efficiency of dairy ruminants. In recent decades, the addition of lipid supplements to ruminant diets has been used to improve energy intake in high-producing dairy cows (Chilliard et al., 1993) and to influence milk FA composition (Doreau et al., 2012). However, certain dietary conditions in dairy cows; (1) diets rich in starch (e.g., high-grain/low-forage diets) and supplemented with PUFA from plants or (2) diets supplemented with PUFA of marine origin (mainly fish oils and algae) cause milk fat depression (MFD; Bauman and Griinari, 2001), whereas others, such as dietary addition of calcium salts from palm oil, increase milk fat content (Mosley et al., 2007).

Different theories have been proposed to explain the causes of MFD. For diets rich in starch and supplemented with vegetable oil (rich in PUFA), the biohydrogenation (BH) theory prevails and attributes MFD to the antilipogenic effect of specific *trans* FA that are

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formed in the rumen, particularly *trans*-10,*cis*-12 CLA (Bauman and Griinari, 2003; Shingfield and Griinari, 2007). For diets including marine supplements, an extension of the BH theory was proposed that includes the role of changes in the availability of long-chain FA in the mammary gland that essentially consist of an increase in the total *trans* 18:1 at the expense of 18:0, which would increase the milk fat melting point and contribute to lower milk fat synthesis (Shingfield and Griinari, 2007; Gama et al., 2008). However, the underlying mechanisms remain poorly documented.

Conversely, regardless of dietary conditions, MFD is not commonly observed in small ruminant species, particularly in goats under dietary conditions similar to those that induce MFD in cows (Shingfield et al., 2010). Differences have been suggested in ruminal PUFA biohydrogenation pathways and mammary lipogenesis by indirect comparisons of the milk fat content and composition in cows (Roy et al., 2006; Shingfield et al., 2003) and goats (Ollier et al., 2009; Toral et al., 2014) fed similar diets, which induce MFD in cows but not in goats. This assumption was evaluated by a direct comparison experiment (Toral et al., 2015) in dairy cows and goats fed similar diets supplemented with sunflower oil and enriched with starch or only supplemented with fish oil. Their study showed interspecies differences in milk fat secretion and FA composition, with both diets inducing MFD in cow; however, surprisingly, MFD was observed in goats under fish oil supplementation at 2% dry DMI, although the degree was lower.

To confirm and complete these findings, the present comparative experiment was designed with the aim to describe the responses of dairy cows and goats to diets supplemented with corn oil and starch (**COS**) or marine algae powder (**MAP**) or hydrogenated palm oil (**HPO**). These dietary treatments have been chosen to either induce MFD for the 2 former or increase fat content in cows for the latter and for which the responses are putative (for COS and HPO) or unknown (for MAP) in goats. Another objective was to identify milk FA biomarkers of the different responses to the MFD diets, which could give insights into the mechanisms involved.

Our hypotheses were that (1) MFD induced by starch and plant oils or marine supplements was due to changes in ruminal (studied by inference with milk *trans* FA) as well as postabsorptive (transport and mammary uptake of FA and lipogenesis) tissue metabolism with different mechanisms involved; (2) diets inducing increased fat content is caused by postabsorptive tissue metabolism; and (3) that these mechanisms and responses differ between ruminant species, with the goat being less sensitive to rumen fermentation changes induced by diet than the cow. To achieve these goals,

the effects of various lipid supplements on dairy performances, milk FA composition, with particular emphasis on *trans*-FA reflecting ruminal PUFA biohydrogenation pathway and plasma metabolites precursors of mammary de novo lipogenesis, were determined on dairy goats and cows.

MATERIALS AND METHODS

Animals, Experimental Design, Diets, and Management

All experimental procedures were approved by the Auvergne Rhône-Alpes Ethics Committee for Experiments on Animals (France; DGRI agreement APAF-IS#3277-2015121411432527 v5), and were compliant with the guidelines established by the European Union Directive 2010/63/EU. Twelve Holstein cows and 12 Alpine goats, all multiparous, nonpregnant, and at the lactation stage of 86 ± 24.9 and 61 ± 1.8 DIM ($\pm$ SD), respectively, were used for the experiment. Cows were housed in a common freestall and goats in individual stalls in separate dedicated facilities at the same research site. Animals were then allocated to 1 of 4 groups (3 cows and 3 goats per group), which were balanced according to DIM, milk production, and milk fat and milk protein content, in a replicated, 4×4 Latin square design to test the effects of 4 treatments that were randomly assigned to each group over four 28-d experimental periods (Kaps and Lamberson, 2009) from February to July 2016.

All animals were offered grass hay ad libitum (first cycle, harvested at the heading stage, and from natural permanent half mountain grassland) supplemented with concentrates containing no additional lipid (control; **CTL**), corn oil (Olvea, Saint Léonard, France) and wheat starch (**COS**), marine algae powder [DHA Gold (*Schizochytrium* sp.), DSM, Basel, Switzerland; **MAP**], or hydrogenated palm oil (Provimi, Cargill, Saint-Germain-En-Laye, France; **HPO**). The formulation, chemical composition, and FA profile of experimental concentrates, with or without lipid supplementation, and grassland hay are reported in Table 1. Concentrates (Neovia, Saint Nolff, France) were composed of cracked corn grain, soybean meal, and pelleted dehydrated alfalfa, except for COS, in which pelleted dehydrated alfalfa was replaced by flattened wheat grain to increase the starch content of that treatment (40% more starch in COS concentrate compared with the CTL concentrate). Lipid supplements were manually mixed with the concentrate immediately before feeding and allocated to the cows and goats as 920 and 111 g/d of corn oil, 310 and 40 g/d of marine algae powder, and 630 and 80 g/d of hydrogenated palm oil, respectively.

Diets were offered as 2 equal meals at 0830 and 1600 h, starting with the concentrate (supplemented or not in lipids) distribution and followed by hay. Concentrate and hay refusals were weighed daily and used to adjust the amounts of feed offered the following day to maintain the targeted dietary forage to concentrate ratio (45:55 on a DM basis). Before starting the experiment, all animals received the CTL diet for a 16-d adaptation period. Animals had access to a constant supply of fresh water ad libitum and were milked at 0800 and 1530 h.

Measurements and Sampling Procedures

Individual feed intake was recorded daily, but only measurements collected during the last week of each experimental period were used for statistical analysis. Representative samples of hay and concentrates were collected weekly during the last 3 wk of each 28-d experimental period, and a subsample was used to determine DM content by drying at 103°C for 48 h. Weekly subsamples were composited by period and species and used to determine chemical composition.

Table 1. Formulation of experimental concentrates and chemical composition of concentrates and forage

Item	Concentrate ¹				Forage
	Control	COS ²	MAP ³	HPO ⁴	Grassland hay
Ingredient, g/kg of DM					
Wheat	—	395	—	—	—
Corn	532	394	518	500	—
Soy	138	150	142	147	—
Dehydrated alfalfa	275	.	283	294	—
Molasses cane	37	35	38	39	—
Dicalcium phosphate	2	2	2	2	—
Carbonate flour	11	19	12	13	—
Salt	3	3	3	3	—
Mineral and vitamin complement	2	2	2	2	—
Chemical composition, g/kg of DM					
OM	923	964	922	932	921
CP	267	264	257	265	142
NDF	198	125	206	206	625
ADF	110	42	113	116	351
Starch	365	507	342	337	—
Ether extract	23	47	26	39	15
14:0	0.04	0.02	0.40	0.24	0.07
16:0	3.91	5.87	4.05	10.87	2.38
<i>cis</i> -9 16:1	0.03	0.05	0.05	0.02	0.02
18:0	0.62	0.78	0.59	8.33	0.20
<i>cis</i> -9 18:1	5.43	11.98	3.98	4.44	0.35
<i>cis</i> -11 18:1	0.23	0.36	0.23	0.18	0.05
18:2n-6	12.6	24.8	8.7	9.7	1.98
18:3n-3	2.01	0.82	2.84	1.62	4.98
20:5n-3	0.003	0.001	0.002	0.002	ND ⁵
22:5n-3	0.05	0.03	0.09	0.04	0.13
22:6n-3	ND	ND	3.06	ND	0.004
Total FA	26.3	45.8	27.1	37.3	12.89
Energy, ⁶ MJ/kg of DM	6.43	7.66	6.51	6.82	4.84
Protein, ⁷ g of PDI /kg of DM	102	104	103	103	55

¹Control = basal concentrate containing no additional oil; COS = basal concentrate containing wheat starch and supplemented with corn oil; MAP = basal concentrate supplemented with marine algae powder of *Schizochytrium* sp.; HPO = basal concentrate supplemented with hydrogenated palm oil. The pellets were manufactured under certain thermal and mechanical conditions: 54°C, 250 kPa, 4-mm section.

²Corn oil (Olvea, Saint Léonard, France) was added to the concentrate at 5% of total DMI and contained [g/kg of total fatty acids (FA)]: 16:0 (114), 18:0 (16.4), *cis*-9 18:1 (297), *cis*-11 18:1 (6.30), 18:2n-6 (535), 18:3n-3 (7.57), 20:0 (3.48), 22:0 (1.0), 24:0 (1.5), and total fatty acids (1,000 g/kg).

³Marine algae powder (DSM, Basel, Switzerland) was added to the concentrate at 1.5% of total DMI and contained (g/kg of total FA): 12:0 (1.12), 14:0 (42.7), 15:0 (1.73), 16:0 (117), *cis*-9 16:1 (0.88), 17:0 (0.29), 18:0 (2.47), *cis*-9 18:1 (0.56), *cis*-11 18:1 (0.55), 18:2n-6 (0.07), 18:3n-3 (0.18), 20:0 (0.17), 20:3n-6 (2.18), 20:4n-6 (2.62), 22:0 (0.24), 22:5n-3 (2.58), 22:6n-3 (370), *cis*-15 24:1 (0.25), and total fatty acids (717 g/kg).

⁴Hydrogenated palm oil (Provimi, Crevin, France) was added to the concentrate at 3% of total DMI and contained (g/kg of total FA): 12:0 (5.09), 14:0 (12.4), 15:0 (0.51), 16:0 (463), 17:0 (1.26), 18:0 (474), *cis*-9 18:1 (11.8), *cis*-11 18:1 (0.71), *cis*-9, *cis*-12 18:2 (0.78), 20:0 (3.39), 20:4 n-6 (3.58), and total fatty acids (995 g/kg).

⁵ND = not detected.

⁶Net energy for lactation calculated according to INRA (2007).

⁷PDI (protein digestible in the intestine) calculated according to INRA (2007).

The milk yields of individual animals were recorded over 6 milkings at 0800 and 1500 h on d 21, 22, and 24 of each experimental period. Simultaneously, milk samples were individually collected and treated with preservative (bronopol-B2; LIAL, Aurillac, France) to measure fat, protein, and lactose. Unpreserved milk samples (2×3 mL) were also collected over 2 consecutive milkings on d 24 of each experimental period and stored at -20°C for FA and lipoprotein lipase (LPL) activity (Bernard et al., 2005) analyses. Blood samples (10 mL) from the jugular vein were collected in evacuated collection tubes containing EDTA (9 mL; Terumo Vacutainer-LML, Nemours, France) from all experimental animals before the morning feeding on d 27 of each experimental period. Plasma recovered after centrifugation ($1,100 \times g$ for 15 min at 4°C) was stored at -20°C until metabolite and insulin concentration analyses.

Chemical Analysis

The chemical composition of the feed ingredients was determined using standard procedures (AOAC International, 1997). Milk fat, protein, and lactose contents were determined by mid-infrared spectrophotometry (LIAL). Fatty acid methyl esters of the feed samples were prepared using a 1-step extraction-transesterification procedure (Sukhija and Palmquist, 1988; adapted by Looor et al., 2004) using 23:0 and 19:0 (Sigma, Saint-Quentin Fallavier, France) as internal standards.

To perform the milk FAME analysis, freeze-dried morning and evening milk samples were pooled according to milk fat yield at each milking to create a representative 100-mg sample for each day. The sample was first incubated with 2 mL of 0.5 M sodium methoxide in anhydrous methanol and 1 mL of hexane at 50°C for 15 min, cooled, and then incubated under the same conditions after adding 1 mL of 37% methanol/hydrochloric acid (95:5 vol/vol). The FAME were then extracted by adding 1.5 mL of hexane and 3 mL of aqueous (6% wt/vol) potassium carbonate and recovered in the hexanoic phase. The FAME from feed and milk samples were injected by autosampler into a GC (Agilent 7890A GC System, Massy, FR) equipped with a flame ionization detector and a CP-Sil 88 capillary column (100 m $\times$ 0.25 mm, 0.2 μm thickness, Agilent Technologies, Inc., Headquarters, Santa Clara, CA).

The FAME profile in a 0.6- μL sample at a 1:52 split ratio was determined using a gradient temperature program (initial oven temperature of 70°C for 1 min, followed by an increase to 100°C at a rate of $5^{\circ}\text{C}/\text{min}$ and maintained for 2 min, an increase to 175°C at a rate of $10^{\circ}\text{C}/\text{min}$ and held for 42 min, and then a $5^{\circ}\text{C}/$

min increase to a final temperature of 225°C that was maintained for 22 min) and hydrogen, which was used as the carrier and fuel gas, at constant pressure (150 kPa). During a second analysis, 18:1 isomers were further resolved using an oven temperature program under isothermal conditions (at 170°C) (Shingfield et al., 2003). Peaks were routinely identified based on comparisons of retention time with commercial authentic standards containing mixtures of FAME (NCP #463, Nu-Chek Prep, Inc., Elysian, MN; Supelco #37, Supelco, Inc., Bellefonte, PA; and O5632, Sigma, Steinheim, Germany) in addition to methyl esters of $\Delta 9$, 12, and 18:2 geometric isomers (L8404; Sigma) and branched-chain *iso*- and *anteiso*-FA from a homemade mixture of commercial standards (Sigma; Matreya, State College, PA; Larodan, Solna, Sweden). Methyl esters that were unavailable as commercial standards were identified based on previous publications (Lerch et al., 2012).

To determine milk CLA composition, the total lipid content of freeze-dried milk was converted to FAME under the same conditions as the FA analysis. The distribution of CLA isomers in the milk samples was determined using an HPLC system (Agilent Technologies 1200 Series) equipped with 3 silver-impregnated silica columns (ChromSpher 5 lipids, 250×4.6 mm, 5- μm particle size; Agilent Technologies Inc.) coupled in series. Methyl esters of CLA were separated under isothermal conditions at 20°C using 0.1% (vol/vol) acetonitrile in heptane at a flow rate of 1 mL/min and monitoring column effluent at 233 and 210 nm (Halmemies-Beauchet-Filleau et al., 2011). Peaks were identified based on a retention profile obtained with positional and geometric CLA isomers (O5632; Sigma).

Milk FA composition was expressed as a weight percentage of total FA. Correction factors to account for the carbon deficiency in the flame ionization detector response for FAME containing 4 to 10 carbon atoms were estimated using milk calibrated with butter oil of known composition (CRM 164; Commission of the European Communities, Community Bureau of Reference, Brussels, Belgium). Concentrations of CLA isomers were calculated based on proportionate peak area responses determined by HPLC and the sum of the *trans*-7,*cis*-9 CLA, *trans*-8,*cis*-10 CLA, and *cis*-9,*trans*-11 CLA weight percentages determined by GC analysis.

Plasma glucose, fatty acids, BHB, urea, acetate, and insulin concentrations were automatically determined by spectrophotometry (ARENA 20XT, Thermo Fisher Scientific, Cergy Pontoise, France) using commercial kits (Glucose GOD-POD, Thermo Scientific, Asnières Sur Seine, France; fatty acids HR2, Sobioda, Montbonnot Saint Martin, France; β -Hydroxybutyrate Kit,

Thermo Scientific; Urea Kit, Thermo Scientific; Acetic Acid, Thermo Scientific; Insulin-CT RIA, CIS Bio International, Gif Sur Yvette, France).

Calculations and Statistical Analysis

Calculations and statistical analyses were performed on measurements from 12 cows and 12 goats. Apparent transfer of 22:6n-3 from DHA Gold was calculated as $[\text{g of milk FA yield} \times (\% \text{ FA in milk fat} - \% \text{ in CTL milk fat})] / (\text{DMI} \times \% \text{ FA in the diet}) \times 100$.

All data were subjected to ANOVA for a 4×4 Latin square design (Kaps and Lamberson, 2009) using the MIXED procedure in SAS (version 9.4, SAS Institute, Inc., Cary, NC). The statistical model included the fixed effects of period, species (Sp), experimental diet (D), the interaction $\text{Sp} \times \text{D}$, and the random effect of individual animal nested within species. For each species, a different variance was used to analyze production data. The differences between means were evaluated using the pdiff option of the LS means statement in the MIXED procedure and adjusted for multiple comparisons using Tukey-Kramer's method, and they were declared significant at $P < 0.05$. P -values > 0.05 and ≤ 0.10 were interpreted as trending toward significance.

RESULTS AND DISCUSSION

Few studies have been performed to achieve a more complete understanding of the nutritional regulation of milk fat secretion with the aim of developing new feeding and management practices to alter milk FA composition and optimize milk fat production in dairy cows (Harvatine et al., 2009; Shingfield et al., 2010) and goats (Chilliard et al., 2014; Bernard et al., 2015). Indirect comparisons of these 2 species have outlined specific responses to some nutritional factors, particularly lipid supplementation (Chilliard et al., 2007). Following that of Toral et al. (2015), the present study is the second direct comparison of dairy cows and goats to date, but it is a more complete examination of the performance and milk FA responses to diets known to induce either bovine milk fat depression or a milk fat increase and for which caprine data are not available.

Diet Composition

By design, in the COS concentrate the energy content was approximately 19% greater than that of the CTL (Table 1). Energy and protein balances were almost positive in all treatments for both species (Table 2). Relative to the CTL, COS increased the energy balance (24%) in cows. In goats, HPO increased the energy bal-

ance (17%) and COS decreased the protein balance by 17%.

Species-Specific Responses to CTL

In the CTL treatment, DMI per kilogram of BW was 43% higher in goats than in cows (Figure 1), and the milk yield per kilogram of BW was higher (38%) for goats than cows (Figure 1). Milk fat, protein, and lactose contents were similar between species in the CTL (Table 2). However, the milk fat composition of cows and goats fed a similar diet based on 45% grassland hay and 55% concentrate clearly highlighted differences among species consistent with data from Toral et al. (2015), who used a control diet based on 40% grassland hay and 60% concentrate. Goat milk contained more $< \text{C16}$ FA (30%) and less $> \text{C16}$ FA (−14%) than that of cow milk (Table 3). Indeed, goat milk is richer in short- and medium-chain FA, caprylic acid (8:0), capric acid (10:0), and lauric acid (12:0), which suggests greater de novo synthesis of these FA in the mammary gland cells of goats compared with cows (Chilliard et al., 2003) (Table 3). In contrast, cow milk contains a higher proportion of long-chain FA, (ΣC18 , Table 3) compared with goats, mainly 18:0, *cis*-9 18:1, *trans*-7, *trans*-9 CLA, and $\Delta 11,13$ CLA, suggesting different ruminal metabolic dietary PUFA pathways or different uptake of these FA by the bovine mammary gland (Tables 3, 4, and 5).

The *cis*-9 14:1/14:0 and *cis*-9 16:1/16:0 desaturation ratios were higher in the milk from cows than that from goats, whereas the opposite was observed in the *cis*-9, *trans*-11 CLA/*trans*-11 18:1 ratio as previously mentioned by Toral et al. (2015). This suggests different availability of *trans*-11 18:1 for the mammary gland or substrate affinity of the mammary Δ -9-desaturase enzyme between species (Table 3).

Response to a Starch-Rich Diet plus Corn Oil

Corn oil and starch supplements lowered DMI in cows (−17%) but not in goats (Table 2), which agreed with the previous comparative study of cows and goats (Toral et al., 2015); this finding may suggest differences in feeding behavior or salivation or an effect of starch on rumen fermentation among species. Otherwise, the COS treatment similarly decreased DMI (by 15%) in both species when expressed per kilogram of BW (Figure 1).

By design, compared with the CTL in both species, the inclusion of COS increased FA intakes by 3 fold, on average, with increases of *cis*-9 18:1 by 6 fold and 18:2n-6 by 4 fold (Table 2). In cows, COS caused a

Table 2. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on intake, milk production, and milk lipoprotein lipase activity in cows and goats¹

Item	Cows				Goats				P-value ²			
	Control	COS	MAP	HPO	Control	COS	MAP	HPO	SEM	Sp	D	Sp × D
Intake, kg/d												
Grassland hay	10.13 ^a	8.12 ^b	9.50 ^a	9.66 ^a	1.09 ^c	0.97 ^c	1.08 ^c	1.15 ^c	0.201	<0.001	<0.001	<0.001
Concentrate + lipid supplement	12.14 ^a	10.41 ^b	11.80 ^a	11.64 ^a	1.46 ^c	1.28 ^c	1.39 ^c	1.50 ^c	0.197	<0.001	<0.001	<0.001
Total DM	22.27 ^a	18.53 ^b	21.30 ^a	21.31 ^a	2.55 ^c	2.24 ^c	2.47 ^c	2.65 ^c	0.393	<0.001	<0.001	<0.001
OM	20.54 ^a	17.29 ^b	19.54 ^a	19.61 ^a	2.35 ^c	2.09 ^c	2.26 ^c	2.44 ^c	0.362	<0.001	<0.001	<0.001
CP	4.69 ^a	3.66 ^c	4.81 ^a	4.29 ^b	0.54 ^d	0.44 ^d	0.56 ^d	0.54 ^d	0.079	<0.001	<0.001	<0.001
NDF	8.74 ^a	6.26 ^b	8.31 ^a	8.31 ^a	0.97 ^c	0.75 ^c	0.95 ^c	1.01 ^c	0.160	<0.001	<0.001	<0.001
Starch	4.43 ^b	4.81 ^a	3.96 ^c	3.71 ^c	0.53 ^d	0.59 ^d	0.47 ^d	0.48 ^d	0.074	<0.001	<0.001	<0.001
Fatty acid intake, g/d												
12:0	0.4 ^c	0.3 ^{cd}	0.9 ^b	3.6 ^a	0.05 ^e	0.03 ^e	0.1 ^d	0.4 ^c	0.017	<0.001	<0.001	<0.001
14:0	1.2 ^{cd}	1.0 ^d	14.5 ^a	9.0 ^b	0.1 ^e	0.1 ^e	1.7 ^c	1.1 ^d	0.066	<0.001	<0.001	<0.001
15:0	0.5 ^c	0.4 ^d	1.0 ^a	0.8 ^b	0.1 ^f	0.05 ^f	0.1 ^e	0.1 ^e	0.006	<0.001	<0.001	<0.001
16:0	64.2 ^d	151.5 ^b	96.3 ^c	353.3 ^a	7.4 ^g	19.0 ^f	11.2 ^g	43.0 ^e	1.76	<0.001	<0.001	<0.001
<i>cis</i> -9 16:1	0.5 ^c	1.2 ^a	0.9 ^b	0.4 ^c	0.06 ^f	0.14 ^d	0.11 ^e	0.05 ^f	0.007	<0.001	<0.001	<0.001
17:0	0.7 ^c	0.9 ^b	0.7 ^c	1.4 ^a	0.07 ^f	0.12 ^e	0.09 ^f	0.18 ^d	0.009	<0.001	<0.001	<0.001
18:0	8.3 ^{cd}	20.0 ^c	9.4 ^{cd}	307.4 ^a	1.0 ^d	2.7 ^d	1.1 ^d	37.2 ^b	1.43	<0.001	<0.001	<0.001
<i>cis</i> -9 18:1	57.3 ^b	311.8 ^a	49.5 ^{bc}	57.9 ^b	6.8 ^d	38.8 ^c	5.8 ^d	7.4 ^d	1.39	<0.001	<0.001	<0.001
<i>cis</i> -11 18:1	2.8 ^b	8.1 ^a	3.3 ^b	2.9 ^b	0.3 ^d	1.0 ^c	0.4 ^d	0.4 ^d	0.041	<0.001	<0.001	<0.001
18:2n-6	145.9 ^b	605.3 ^a	120.3 ^b	128.2 ^b	17.2 ^d	75.1 ^c	14.1 ^d	16.3 ^d	2.76	<0.001	<0.001	<0.001
18:3n-3	74.4 ^{ab}	56.6 ^c	84.0 ^a	70.0 ^b	8.2 ^{de}	6.8 ^c	9.7 ^d	8.5 ^{de}	0.724	<0.001	<0.001	<0.001
20:0	2.4 ^b	4.6 ^a	2.5 ^b	4.4 ^a	0.3 ^d	0.6 ^c	0.3 ^d	0.5 ^c	0.032	<0.001	<0.001	<0.001
20:2n-6	0.3 ^b	0.4 ^a	0.3 ^b	0.3 ^b	0.03 ^d	0.05 ^c	0.03 ^d	0.03 ^d	0.003	<0.001	<0.001	<0.001
20:4n-6	ND ³	ND	1.1	2.3	ND	ND	0.13	0.27	0.011	<0.001	—	—
22:0	2.7	2.7	3.0	3.0	0.3	0.3	0.3	0.4	0.027	<0.001	0.035	0.140
20:5n-3	ND	ND	1.1	2.26	ND	ND	0.13	0.273	0.469	<0.001	—	—
22:5n-3	2.0 ^b	1.7 ^b	3.0 ^a	1.9 ^b	0.2 ^d	0.2 ^d	0.3 ^c	0.2 ^d	0.021	<0.001	<0.001	<0.001
22:6n-3	0.05 ^c	0.5 ^c	115.5 ^a	0.04 ^c	0.01 ^c	0.07 ^c	13.4 ^b	0.01 ^c	0.417	<0.001	<0.001	<0.001
Total FA	400.6 ^d	1,206.2 ^a	603.4 ^c	995.8 ^b	46.3 ^h	149.9 ^e	70.1 ^g	122.1 ^f	7.26	<0.001	<0.001	<0.001
Yield												
Milk, kg/d	27.8	25.0	26.5	27.1	3.1	3.0	2.9	3.0	0.690	<0.001	0.102	0.113
Fat, g/d	944 ^a	474 ^c	703 ^b	1,031 ^a	106 ^d	101 ^d	84 ^d	107 ^d	27.3	<0.001	<0.001	<0.001
Protein, g/d	864	814	819	819	100	101	96	97	16.5	<0.001	0.433	0.485
Lactose, g/d	1,462	1,279	1,315	1,391	153	157	146	148	36.7	<0.001	0.059	0.053
Concentration, g/100 g												
Fat	3.39 ^{bc}	1.85 ^e	2.64 ^d	3.82 ^a	3.47 ^{ab}	3.45 ^{ab}	2.95 ^{cd}	3.62 ^{ab}	0.907	0.002	<0.001	<0.001
Protein	3.08 ^b	3.29 ^a	3.12 ^{ab}	3.03 ^b	3.35 ^{ab}	3.37 ^{ab}	3.41 ^{ab}	3.36 ^{ab}	0.946	0.086	0.024	0.043
Lactose	5.21 ^a	5.04 ^{ab}	4.97 ^b	5.15 ^a	4.98 ^{ab}	5.14 ^{ab}	5.05 ^{ab}	5.01 ^{ab}	0.404	0.448	0.120	<0.001
Milk LPL ⁴ activity, nmol/min per mL	547	478	496	471	431	380	399	373	3.87	<0.001	<0.001	0.565
BW, kg	678	686	678	676	54	53	54	54	11.3	<0.001	0.227	0.158
Energy balance, ⁵ %	95 ^d	118 ^{ab}	104 ^{cd}	98 ^d	105 ^{bcd}	111 ^{abcd}	114 ^{abc}	123 ^a	2.78	0.023	<0.001	<0.001
Protein balance, ⁶ %	113 ^{bc}	112 ^{bc}	126 ^{ab}	104 ^c	126 ^{ab}	105 ^c	138 ^a	131 ^{ab}	3.42	0.031	<0.001	<0.001

^{a-h}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).³ND = not detected.⁴LPL = lipoprotein lipase.⁵Net energy for lactation balance (MJ/d) calculated according to INRA (2007) and expressed as a percent of estimated requirements.⁶Protein balance (g of protein digestible in the intestine/d) calculated according to INRA (2007) and expressed as a percent of estimated requirements.

dramatic decrease in milk fat content (-45%) and yield (-10%) (Table 2), which is commonly observed in cows fed high-starch diets containing vegetable oils (Piperova et al., 2000; Peterson et al., 2003; Roy et al., 2006). Conversely, no adverse effects on milk fat content and yield were observed in goats (Table 2), which was consistent with previous studies of goats (Bernard et al., 2009; Chilliard et al., 2014).

Changes in the daily secretion of short- and medium-chain ($<C16$ and $C16$) and long-chain FA ($>C16$) expressed as millimoles per kilogram of BW are shown in Figure 1. In goats, COS lowered the yields of FA synthesized de novo (the sums of $<C16$ FA was decreased by 25%), but this decrease was compensated by an increase in the secretion of long-chain FA assimilated from blood (the sum of $>C16$ FA was increased by

45%). Similarly, COS lowered the yields of milk short- and medium-chain FA secretion in cows (-68%), which was not compensated by an increase in the output of long-chain FA, as observed in Toral et al. (2015) with a starch-rich diet and sunflower oil. These differences in the responses to diets containing relatively high amounts of starch and PUFA that induce MFD in cows but not in goats may be due, at least in part, to species-specific differences in the synthesis of ruminal biohydrogenation (RBH) intermediates with antilipogenic effects and in their postabsorptive tissue metabolism as the uptake by and sensitivity of the mammary gland to these compounds (Chilliard et al., 2007; Shingfield et al., 2010). In the present study, the responses of both species to COS were characterized by higher concentrations of *trans*-10,*cis*-12 CLA, *trans*-7,*cis*-9 CLA, *trans*-

Figure 1. Daily DMI and the yields of milk, milk fat, and major groups of fatty acids (FA) expressed on a kilograms of BW basis in cows and goats fed a basal diet containing no additional lipid (control), or supplemented with corn oil and starch (COS), marine algae powder (MAP), or hydrogenated palm oil (HPO). Within each parameter, values not sharing a common letter (a–f) differ at $P < 0.05$. The group of FA $<C16$ represents FA synthesized de novo, those of $>C16$ represent preformed FA taken up from circulation, and $C16$ FA are derived from both sources. SEM: DMI = 1.173, milk yield = 3.115, fat yield = 0.096, $<C16$ = 0.201, $C16$ = 0.105, and $>C16$ = 0.113.

Table 3. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on milk paired chain fatty acid (FA) composition in cows and goats¹

FA, g/100 g of FA	Cows				Goats				P-value ²			
	Control	COS	MAP	HPO	Control	COS	MAP	HPO	SEM	Sp	D	Sp × D
4:0	2.84 ^a	1.46 ^c	3.10 ^a	2.89 ^a	2.01 ^{bc}	1.89 ^{bc}	1.86 ^{bc}	2.18 ^b	0.111	0.001	<0.001	<0.001
6:0	2.31 ^{bcd}	0.84 ^e	2.57 ^a	2.14 ^{cd}	2.58 ^{ab}	2.11 ^d	2.49 ^{abc}	2.55 ^{ab}	0.067	<0.001	<0.001	<0.001
8:0	1.44 ^e	0.45 ^f	1.74 ^d	1.24 ^e	3.11 ^{ab}	2.35 ^c	3.25 ^a	2.93 ^b	0.062	<0.001	<0.001	0.01
10:0	3.33 ^{de}	1.07 ^f	4.20 ^d	2.65 ^e	11.4 ^a	7.86 ^c	12.2 ^a	10.4 ^b	0.166	<0.001	<0.001	0.008
<i>cis</i> -9 10:1	3.33 ^a	0.086 ^c	0.35 ^a	0.28 ^b	0.25 ^b	0.15 ^c	0.24 ^b	0.22 ^b	0.011	0.012	<0.001	<0.001
12:0	3.87	1.65	4.92	3.04	5.90	3.78	7.12	5.11	0.133	<0.001	<0.001	0.965
14:0	12.35 ^b	7.52 ^e	13.98 ^a	10.76 ^{cd}	10.88 ^{cd}	7.87 ^e	11.65 ^{bc}	10.28 ^d	0.189	0.001	<0.001	<0.001
<i>cis</i> -9 14:1	1.23	1.19	1.24	1.03	0.176	0.130	0.191	0.154	0.069	<0.001	0.087	0.237
<i>trans</i> -9 14:1	0.015	0.017	0.017	0.014	0.043	0.029	0.032	0.039	0.003	<0.001	0.554	0.257
16:0	29.40 ^b	22.54 ^d	27.58 ^{bc}	32.42 ^a	26.27 ^c	20.81 ^d	26.28 ^c	28.27 ^{bc}	0.488	0.001	<0.001	0.028
<i>cis</i> -7 16:1	0.14	0.17	0.11	0.15	0.24	0.25	0.22	0.23	0.007	<0.001	<0.001	0.426
<i>trans</i> -6-8 16:1	0.028 ^d	0.051 ^{ab}	0.045 ^{bc}	0.029 ^d	0.036 ^{cd}	0.048 ^{cd}	0.060 ^a	0.038 ^{cd}	0.002	0.009	<0.001	0.016
<i>cis</i> -9 16:1	1.44 ^{bc}	1.98 ^a	1.12 ^c	1.50 ^b	0.55 ^d	0.48 ^d	0.57 ^d	0.56 ^d	0.073	<0.001	<0.001	<0.001
<i>cis</i> -11 16:1	0.041 ^b	0.057 ^a	0.035 ^b	0.030 ^{bc}	0.014 ^{cd}	0.017 ^{cd}	0.015 ^{cd}	0.013 ^d	0.002	<0.001	<0.001	0.008
<i>trans</i> -9 16:1	0.19	0.31	0.42	0.25	0.33	0.39	0.38	0.37	0.030	0.082	0.156	0.462
18:0	8.48 ^{ab}	8.73 ^{ab}	3.33 ^d	10.11 ^a	5.90 ^c	10.57 ^a	1.90 ^d	7.18 ^b	0.369	0.023	<0.001	<0.001
18:3n-6	0.028	0.016	0.025	0.026	0.041	0.021	0.028	0.028	0.004	0.259	0.209	0.857
18:3n-3	0.66 ^a	0.35 ^d	0.53 ^{bc}	0.56 ^{bc}	0.62 ^{ab}	0.51 ^c	0.51 ^c	0.57 ^{abc}	0.013	0.167	<0.001	<0.001
Sum	26.15 ^d	12.99 ^f	30.49 ^c	22.73 ^e	35.92 ^{ab}	25.86 ^{de}	38.55 ^a	33.46 ^{bc}	0.431	<0.001	<0.001	0.006
Σ 4:0-14:0	29.86 ^d	15.78 ^f	34.27 ^c	25.93 ^e	38.83 ^{ab}	28.58 ^{de}	41.73 ^a	36.09 ^{bc}	0.440	<0.001	<0.001	0.004
Σ <16:0	36.88	56.36	33.21	38.17	31.71	46.98	27.53	32.61	0.764	<0.001	<0.001	0.119
Σ 16:0 + <i>cis</i> -9 16:1	30.84 ^b	24.52 ^d	28.69 ^{bc}	33.92 ^a	26.82 ^{cd}	21.30 ^e	26.85 ^{cd}	28.83 ^{bc}	0.520	<0.001	<0.001	0.035
Σ C18	34.95	54.76	29.44	36.45	29.94	45.38	24.75	31.01	0.747	<0.001	<0.001	0.075
Σ 18:0 + <i>cis</i> -9 18:1	24.96	30.83	10.35	27.87	19.26	27.59	7.48	21.70	0.650	<0.001	<0.001	0.324
Σ <i>cis</i> 18:1	18.06	24.85	8.98	19.19	14.88	19.01	7.00	15.91	0.446	<0.001	<0.001	0.189
Σ <i>trans</i> 18:1	3.22 ^d	14.18 ^a	10.03 ^b	2.84 ^d	3.13 ^d	6.17 ^c	8.27 ^{bc}	2.84 ^d	0.324	<0.001	<0.001	<0.001
Σ ≥20:0	0.99 ^c	0.87 ^c	2.88 ^a	0.93 ^c	0.77 ^c	0.82 ^c	1.81 ^b	0.70 ^c	0.047	<0.001	<0.001	<0.001
Ratio												
<i>trans</i> -10 18:1/ <i>trans</i> -11 18:1	0.46 ^b	4.64 ^a	0.63 ^b	0.44 ^b	0.32 ^b	0.78 ^b	0.34 ^b	0.40 ^b	0.103	<0.001	<0.001	<0.001
C18:2n-6/C18:3n-3	3.96 ^{bc}	8.42 ^a	4.03 ^{bc}	3.75 ^c	5.21 ^b	7.99 ^a	4.95 ^{bc}	4.88 ^{bc}	0.153	0.003	<0.001	0.028
<i>cis</i> -9 14:1/14:0	0.098 ^b	0.16 ^a	0.088 ^b	0.10 ^b	0.016 ^c	0.015 ^c	0.016 ^c	0.015 ^c	0.006	<0.001	<0.001	<0.001
<i>cis</i> -9 16:1/16:0	0.049 ^b	0.087 ^a	0.041 ^b	0.047 ^b	0.021 ^c	0.023 ^c	0.022 ^c	0.020 ^c	0.003	<0.001	<0.001	<0.001
<i>cis</i> -9 18:1/18:0	2.00 ^{bc}	2.67 ^{ab}	2.57 ^{abc}	1.78 ^c	2.29 ^{bc}	1.71 ^{bc}	3.44 ^a	2.05 ^{bc}	0.137	0.564	<0.001	<0.001
<i>cis</i> -9, <i>trans</i> -11 CLA/ <i>trans</i> -11 18:1	0.37 ^{cd}	0.42 ^{bcd}	0.33 ^d	0.38 ^{cd}	0.57 ^{ab}	0.47 ^{bcd}	0.63 ^a	0.50 ^{bc}	0.027	<0.001	0.482	<0.001
Apparent transfer, %												
22:6 n-3			11.9				7.3					

^{a-f}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).³Calculated as [grams of milk fat yield × (% FA in milk fat – % FA in control milk fat)/(DMI × % FA in the diet)] × 100.

Table 4. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on milk 18:1 isomer fatty acid (FA) concentration in cows and goats¹

FA, g/100 g of FA	Cows				Goats				P-value ²	
	Control	COS	MAP	HPO	Control	COS	MAP	HPO		
	SEM	SEM	SEM	SEM	SEM	SEM	SEM	SEM	Sp	Sp × D
<i>cis</i> -9 18:1	16.48	22.10	7.02	17.76	13.36	17.04	5.58	14.52	<0.001	0.264
<i>cis</i> -10 18:1	0.44 ^b	0.72 ^a	0.76 ^a	0.45 ^b	0.39 ^b	0.50 ^b	0.40 ^b	0.37 ^b	<0.001	<0.001
<i>cis</i> -11 18:1	0.51 ^b	0.79 ^a	0.50 ^b	0.45 ^b	0.47 ^b	0.52 ^b	0.43 ^b	0.41 ^b	0.006	0.047
<i>cis</i> -12 18:1	0.26 ^{bc}	0.61 ^a	0.17 ^c	0.20 ^c	0.32 ^{bc}	0.46 ^{ab}	0.16 ^c	0.30 ^{bc}	0.959	0.050
<i>cis</i> -13 18:1	0.13	0.23	0.16	0.14	0.10	0.20	0.14	0.10	0.118	0.924
<i>cis</i> -16 18:1 ³	0.074 ^c	0.19 ^a	0.18 ^a	0.058 ^e	0.083 ^c	0.15 ^{ab}	0.13 ^b	0.076 ^c	0.022	0.001
<i>cis</i> -15 18:1 ⁴	0.17	0.19	0.18	0.14	0.16	0.14	0.15	0.15	0.148	0.350
<i>cis</i> -6 + <i>trans</i> -12 18:1	0.4	1.03	1.13	0.32	0.31	2.73	0.67	0.3	0.557	0.396
<i>cis</i> -14 + <i>trans</i> -16 18:1	0.32 ^c	0.47 ^b	0.69 ^a	0.30 ^c	0.24 ^c	0.32 ^c	0.28 ^c	0.21 ^c	0.015	0.084
<i>trans</i> -4 18:1	0.016 ^d	0.064 ^a	0.032 ^{bc}	0.012 ^d	0.012 ^d	0.037 ^b	0.018 ^{cd}	0.011 ^d	<0.001	0.002
<i>trans</i> -5 18:1	0.017	0.058	0.044	0.041	0.25	0.024	0.43	0.19	0.105	0.620
<i>trans</i> -6-8 18:1	0.29	1.33	0.65	0.31	0.24	0.68	0.83	0.26	0.268	0.133
<i>trans</i> -9 18:1	0.26 ^c	0.91 ^a	0.89 ^a	0.29 ^c	0.27 ^c	0.52 ^b	0.61 ^b	0.30 ^c	<0.001	<0.001
<i>trans</i> -10 18:1	0.63 ^c	8.60 ^a	2.56 ^b	0.50 ^c	0.47 ^c	1.68 ^{bc}	1.30 ^{bc}	0.45 ^c	<0.001	<0.001
<i>trans</i> -11 18:1	1.39	1.89	4.17	1.15	1.46	2.47	4.31	1.22	0.252	0.629
<i>trans</i> -13 18:1	0.62 ^{cde}	1.33 ^b	1.69 ^a	0.53 ^{de}	0.43 ^c	0.74 ^{cd}	0.77 ^c	0.41 ^e	<0.001	<0.001

^{a-e}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).³Coelutes with *cis*-9, *trans*-12 18:2.⁴Coelutes with 19:0.

8, *trans*-10 CLA, and *trans*-10, *trans*-12 CLA compared with the CTL (Table 5 and Figure 2). In cows, with COS treatment the large increases in *trans*-7, *cis*-9 CLA, *trans*-9, *trans*-11 CLA, and *trans*-10, *trans*-12 CLA (316, 69, and 728%, respectively), were correlated with a decrease in milk fat content ($r = -0.928$, $n = 24$, $P < 0.001$; $r = -0.768$, $n = 24$, $P < 0.001$; and $r = -0.768$, $n = 24$, $P < 0.001$, respectively) that was probably due to a concomitant synthesis of these CLA isomers with *trans*-10, *cis*-12 CLA rather than an antilipogenic effect per se (Saebø et al., 2005; Perfield et al., 2006). Indeed, among these RBH intermediates, *trans*-10, *cis*-12 CLA was shown to unequivocally inhibit milk fat synthesis (Shingfield et al., 2010). In cows under COS treatment, the milk concentration of this CLA isomer increased by 17 fold compared with the CTL, but the increase in goats was lower (by 6 fold) and not significant due to high individual variability (Table 5 and Figure 2). In cows, the magnitude of the alteration in *trans*-10, *cis*-12 CLA was similar in response to the COS treatment in this study and the sunflower oil and starch diet in Toral et al. (2015) despite a lower starch and 18:2n-6 intake with COS (0.59 and 75.1 g/d, respectively; Table 2) compared with the starch-rich diet and sunflower oil (0.70 and 93.7 g/d, respectively). However, previous reports suggest that *trans*-10, *cis*-12 CLA in the mammary gland does not, in isolation, fully explain MFD in cows (Shingfield et al., 2010), and that other RBH intermediates, such as *trans*-10 18:1, could also be implicated in diet-induced MFD (Shingfield and Griinari, 2007) even though results of the few studies on the effects of *trans*-10 18:1 on lipogenesis in cows are unclear (Lock et al., 2007; Kadegowda et al., 2009; Shingfield et al., 2009). In the present study, COS increased the *trans*-10 18:1 isomer concentration in the cow milk by 13 fold compared with the CTL, and to a lower extent (by 3 fold) in goat milk (Table 4), and lead to an increase in the *trans*-10 18:1/*trans*-11 18:1 ratio (Table 3) only in cows. These increases in the concentration of *trans*-10 18:1 and of the *trans*-10 18:1/*trans*-11 18:1 ratio may be considered biomarkers of altered RBH pathways in cows but are not always a useful diagnostic of rumen alteration in goats, as previously shown (Shingfield et al., 2010; Martínez Marín et al., 2012; Bernard et al., 2015). However, in the previous comparative study by Toral et al. (2015), a shift occurs from *trans*-11 18:1 to *trans*-10 18:1 with sunflower oil and starch supplementation in goats, whereas no variation of milk fat content was observed, with significant increases in both *trans*-10, *cis*-12 CLA and *trans*-10 18:1 isomers; however, the effect for the latter was far more pronounced in cows. These differences in the occurrence of *trans*-10 isomers in goats in the present study and in Toral et al. (2015) may be explained, at least in part, by large in-

Table 5. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on milk 18:2 isomer fatty acid (FA) concentrations in cows and goats¹

FA, mg/100 g of FA	Cows				Goats				<i>P</i> -value ²			
	Control	COS	MAP	HPO	Control	COS	MAP	HPO	SEM	Sp	D	Sp × D
<i>cis</i> -9, <i>cis</i> -12 18:2	2,590	2,940	2,120	2,090	3,220	3,940	2,490	2,760	91.31	<0.001	<0.001	0.167
<i>cis</i> -9, <i>trans</i> -13 18:2 ³	200 ^b	460 ^a	430 ^a	160 ^b	250 ^b	360 ^a	380 ^a	220 ^b	17.18	0.692	<0.001	0.001
<i>cis</i> -9, <i>trans</i> -14 18:2	94 ^{ef}	190 ^a	180 ^{ab}	64 ^f	110 ^{de}	150 ^{bc}	140 ^{cd}	86 ^{ef}	5.715	0.145	<0.001	<0.001
<i>trans</i> -9, <i>cis</i> -12 18:2	28	94	62	27	85	58	48	24	10.07	0.938	0.102	0.130
<i>trans</i> -11, <i>cis</i> -15 18:2	96 ^b	110 ^b	190 ^a	84 ^b	100 ^b	56 ^b	190 ^a	84 ^b	8.676	0.269	<0.001	0.050
<i>trans</i> -9, <i>trans</i> -12 18:2	24	40	46	31	25	29	39	10	5.409	0.226	0.003	0.353
<i>trans</i> -10, <i>trans</i> -14 18:2	62	100	62	50	30	51	54	40	6.386	0.008	0.072	0.322
<i>trans</i> -11, <i>trans</i> -15 18:2	28	66	39	20	18	31	33	12	4.146	0.018	<0.001	0.216
<i>cis</i> -9, <i>trans</i> -11 CLA ⁴	509 ^d	773 ^{cd}	1,375 ^b	446 ^d	842 ^{bcd}	1,177 ^{bc}	2,537 ^a	617 ^d	85.64	<0.001	<0.001	<0.001
<i>cis</i> -11, <i>trans</i> -13 CLA	1.03 ^{bc}	1.91 ^a	1.28 ^{ab}	0.71 ^{bc}	0.68 ^{bc}	0.66 ^{bc}	1.37 ^{ab}	0.38 ^c	0.118	0.011	<0.001	0.009
<i>trans</i> -7, <i>cis</i> -9 CLA	36 ^c	150 ^a	103 ^b	31 ^c	53 ^c	88 ^b	95 ^b	41 ^c	3.132	0.019	<0.001	<0.001
<i>trans</i> -8, <i>cis</i> -10 CLA	9.43 ^b	26.81 ^a	9.50 ^b	9.88 ^b	5.83 ^b	8.53 ^b	11.71 ^b	5.38 ^b	1.626	0.010	0.009	0.019
<i>trans</i> -10, <i>cis</i> -12 CLA	3.76 ^b	69.03 ^a	3.73 ^b	3.53 ^b	2.26 ^b	15.78 ^b	2.42 ^b	1.81 ^b	1.969	<0.001	<0.001	<0.001
<i>trans</i> -11, <i>cis</i> -13 CLA	1.03 ^{bc}	1.91 ^a	1.28 ^{ab}	0.71 ^{bc}	0.68 ^{bc}	0.66 ^{bc}	1.37 ^{ab}	0.38 ^c	0.118	0.011	<0.001	0.009
<i>trans</i> -12, <i>cis</i> -14 CLA	2.33 ^{ab}	2.93 ^{ab}	3.53 ^a	2.03 ^{ab}	2.62 ^{ab}	1.88 ^b	1.78 ^b	2.06 ^{ab}	0.180	0.018	0.392	0.020
<i>trans</i> -7, <i>trans</i> -9 CLA	6.38	7.82	8.85	6.03	3.98	5.51	6.53	3.47	0.202	<0.001	<0.001	0.988
<i>trans</i> -8, <i>trans</i> -10 CLA	2.73 ^d	12.13 ^a	8.48 ^b	2.68 ^d	3.91 ^{cd}	6.66 ^b	6.15 ^{bc}	3.38 ^d	0.301	0.002	<0.001	<0.001
<i>trans</i> -9, <i>trans</i> -11 CLA	8.25	13.92	20.00	6.75	7.32	12.57	17.14	5.33	0.750	0.136	<0.001	0.907
<i>trans</i> -10, <i>trans</i> -12 CLA	3.51 ^c	29.06 ^a	4.70 ^{bc}	3.10 ^c	2.46 ^c	9.38 ^b	2.48 ^c	1.96 ^c	0.650	<0.001	<0.001	<0.001
<i>trans</i> -11, <i>trans</i> -13 CLA	8.10 ^b	11.38 ^a	11.76 ^a	8.08 ^b	4.28 ^c	3.25 ^c	3.77 ^c	3.84 ^c	0.461	<0.001	0.018	0.001
<i>trans</i> -12, <i>trans</i> -14 CLA	4.61 ^b	3.88 ^{bc}	8.29 ^a	3.80 ^{bc}	2.57 ^{bcd}	1.12 ^d	2.47 ^{bcd}	2.12 ^{cd}	0.255	<0.001	<0.001	<0.001

^{a-f}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.
¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.
²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).
³Coelutes with *cis*-10, *trans*-14 18:2.
⁴Coelutes with *trans*-9, *cis*-11 18:2.

Figure 2. Milk 18:0, *trans*-10 18:1, *trans*-11 18:1, *cis*-11 18:1, *cis*-9 18:1, *trans*-10,*cis*-12 CLA, *cis*-9,*trans*-11 CLA, and 16:0 concentrations in cows and goats fed a basal diet containing no additional lipid (control), or supplemented with corn oil and starch (COS), marine algae powder (MAP), or hydrogenated palm oil (HPO). Within each fatty acid, values not sharing a common letter (a–d) differ at $P < 0.05$. SEM: 18:0 = 0.369, *trans*-10 18:1 = 0.239, *trans*-11 18:1 = 0.130, *cis*-11 18:1 = 0.024, *cis*-9 18:1 = 0.449, *trans*-10,*cis*-12 CLA = 0.002, *cis*-9,*trans*-11 CLA = 0.086, and 16:0 = 0.488.

dividual differences in the susceptibility of goats to the development of a *trans*-10 shift, as previously observed (Bernard et al., 2009), and to lower starch and 18:2n-6 intake with COS in the present study compared with the starch-rich diet and sunflower oil in Toral et al. (2015), as mentioned above.

The COS treatment-specific decreases in milk odd and branched-chain FA (**OBCFA**) in cows (*iso*-14:0, 15:0, *anteiso*-15:0, and *iso*-16:0; Table 6) were negatively correlated (results not shown) with increases in milk *trans*-10-18:1 and 18:2 isomers, showing that changes in OBCFA may also be considered potential tools for diagnosing rumen function (e.g., rumen fermentation pattern), as proposed by Vlaeminck et al. (2006). Indeed, dietary factors, such as the alteration of the ruminal pH and microbial population by COS treatment, affect the ruminal biohydrogenation path-

ways of dietary FA and thus the *trans*-FA and OBCFA in the milk profile (Kargart et al., 2017).

With COS treatment, the substantial decrease (by a mean of 41%) in plasma acetate and BHB (precursor of *de novo* lipogenesis) in cows could contribute, at least in part, to between-species variations in the response of milk fat to COS treatment, despite a decrease (by a mean of 31%) in goats (Table 7). Indeed, the decrease in rumen acetate and butyrate production may limit milk fat synthesis but cannot be responsible alone for the reduced milk fat synthesis with MFD diets because others mechanisms are also involved (Bauman and Griinari, 2003). Furthermore, the decrease in circulating BHB in goats with COS was not accompanied by changes in milk fat yield.

In addition to their antilipogenic effects, some RBH intermediates have been reported to have inhibiting ac-

Table 6. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on milk odd- and branched-chain fatty acid (FA) composition in cows and goats¹

FA, g/100 g of FA	Cows				Goats				SEM	<i>P</i> -value ²		
	Control	COS	MAP	HPO	Control	COS	MAP	HPO		Sp	D	Sp × D
5:0	0.026 ^b	0.024 ^b	0.026 ^b	0.027 ^b	0.031 ^b	0.050 ^a	0.033 ^b	0.029 ^b	0.001	<0.001	0.001	<0.001
7:0	0.022 ^c	0.015 ^c	0.023 ^c	0.023 ^c	0.059 ^b	0.091 ^a	0.072 ^{ab}	0.056 ^b	0.002	<0.001	0.012	<0.001
9:0	0.026 ^d	0.015 ^d	0.030 ^d	0.022 ^d	0.12 ^{bc}	0.17 ^a	0.15 ^{ab}	0.11 ^c	0.005	<0.001	0.005	0.001
11:0	0.043 ^c	0.021 ^c	0.054 ^c	0.031 ^c	0.19 ^{ab}	0.24 ^a	0.26 ^a	0.16 ^b	0.0084	<0.001	0.001	0.010
13:0 ³	0.20	0.11	0.23	0.15	0.30	0.25	0.37	0.24	0.012	<0.001	<0.001	0.165
<i>anteiso</i> 13:0	0.014	0.012	0.013	0.018	0.014	0.010	0.015	0.013	0.001	0.408	0.051	0.202
<i>iso</i> 13:0	0.036	0.025	0.037	0.032	0.023	0.018	0.018	0.020	0.001	<0.001	0.040	0.254
<i>iso</i> 14:0	0.083 ^a	0.046 ^c	0.064 ^b	0.084 ^a	0.083 ^{ab}	0.083 ^{ab}	0.075 ^{ab}	0.079 ^{ab}	0.0038	0.061	<0.001	<0.001
15:0	0.98	0.76	1.03	0.84	1.09	1.04	1.17	0.98	0.041	0.007	<0.001	0.307
<i>anteiso</i> 15:0	0.47 ^a	0.35 ^b	0.46 ^a	0.43 ^a	0.32 ^b	0.31 ^b	0.35 ^b	0.32 ^b	0.013	<0.001	<0.001	0.005
<i>iso</i> 15:0	0.24 ^a	0.12 ^c	0.21 ^{ab}	0.22 ^{ab}	0.20 ^b	0.15 ^c	0.20 ^{ab}	0.21 ^{ab}	0.0053	0.372	<0.001	0.001
<i>iso</i> 16:0	0.22 ^b	0.15 ^c	0.23 ^{ab}	0.21 ^b	0.23 ^b	0.30 ^a	0.24 ^b	0.22 ^b	0.011	0.017	0.620	<0.001
17:0	0.74	0.48	0.73	0.61	0.83	0.62	0.83	0.73	0.018	<0.001	<0.001	0.541
<i>anteiso</i> 17:0	0.45	0.38	0.44	0.36	0.36	0.36	0.36	0.34	0.015	0.019	0.028	0.183
<i>iso</i> 17	0.33	0.58	0.40	0.22	0.20	0.42	0.52	0.19	0.034	0.313	<0.001	0.151
<i>cis</i> -9 17:1	0.21 ^{ab}	0.25 ^a	0.15 ^c	0.18 ^{bc}	0.18 ^{bc}	0.14 ^c	0.14 ^c	0.17 ^{bc}	0.0091	0.004	<0.001	<0.001
<i>iso</i> 18:0	0.052	0.034	0.043	0.043	0.034	0.032	0.041	0.037	0.002	0.024	0.053	0.135
23:0	0.033 ^{ab}	0.014 ^b	0.055 ^a	0.031 ^{ab}	0.040 ^{ab}	0.012 ^b	0.023 ^b	0.020 ^b	0.0037	0.080	0.003	0.046

^{a-d}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.

¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.

²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).

³Coelutes with *cis*-9 12:1.

tion on $\Delta 9$ -desaturase activity including *trans*-9,*trans*-11 CLA, *trans*-10,*trans*-12 CLA, and *trans*-10,*cis*-12 CLA (Bernard et al., 2013). Among these CLA isomers, milk fat concentrations of the latter 2 were increased in cows with the COS treatments, whereas only *trans*-10,*trans*-12 increased in goats (Table 5). These observations are not consistent with the significant increase in the 14- and 16-carbon FA concentration ratios for $\Delta 9$ -desaturase in milk from cows supplemented with COS, whereas no changes were observed in goats according to previous direct comparison data (Toral et al., 2015). This suggests both a low disponibility of *trans*-9,*trans*-11 CLA in the mammary gland and dif-

ferences in sensitivity to the inhibitory effect of *trans*-10,*trans*-12-, and *trans*-10,*cis*-12 CLA among species.

These different findings suggest that, in cows, MFD due to starch-rich diet plus corn oil is the result of a set of factors (large synthesis of RBH intermediates with antilipogenic effects, low occurrence of de novo lipogenesis precursors, and so on), of which the sum of the effects induces decreased milk fat content, as opposed to a single factor. In particular, the ruminal and intermediary (plasma FA transport) lipid metabolism of goats and cows receiving starch-rich diets supplemented with plant oils would need to be further studied to clarify these hypothesis.

Table 7. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on plasma metabolite and hormone concentrations in cows and goats¹

Item	Cows				Goats				SEM	<i>P</i> -value ²		
	Control	COS	MAP	HPO	Control	COS	MAP	HPO		Sp	D	Sp × D
Glucose, g/L	0.715	0.730	0.671	0.716	0.646	0.660	0.667	0.636	0.0191	0.051	0.364	0.047
Fatty acids, mM	0.115	0.156	0.097	0.111	0.191	0.258	0.102	0.129	0.0180	0.061	<0.001	0.146
Acetate, mM	0.378	0.225	0.335	0.416	0.259	0.181	0.280	0.310	0.0149	0.001	<0.001	0.347
BHB, mM	0.607 ^{ab}	0.356 ^{cd}	0.592 ^{ab}	0.648 ^a	0.444 ^{bc}	0.301 ^d	0.456 ^{bc}	0.459 ^{bc}	0.0308	0.005	<0.001	0.046
Urea, g/L	0.179	0.149	0.207	0.189	0.408	0.399	0.402	0.412	0.0151	<0.001	0.195	0.314
Insulin, μ IU/mL	21.1	19.9	16.1	21.9	17.2	18.4	18.2	20.3	0.947	0.367	0.055	0.193

^{a-d}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.

¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.

²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).

Response to a Diet Supplemented with Marine Algae Powder

In recent decades, algae supplements have been used to improve the milk quality of dairy cows due to their high contents of long-chain n-3 PUFA (Franklin et al., 1999; Angulo et al., 2012; Bichi et al., 2013). Marine algae may be considered an emerging dietary resource because they are environmentally sustainable (by increasing the land area available for the cultivation of other resources) and of plant origin (which is more acceptable for the ruminant diet than fish oil).

In the present study, supplementation with MAP did not adversely affect DMI in either species (Table 2), as was previously demonstrated in cows (Stamey et al., 2012), although decreased intake has been observed with unprotected marine algae supplements (Franklin et al., 1999; Offer et al., 2001; Boeckaert et al., 2008). Depending on the type of marine product, the effects on DMI may differ. In Toral et al. (2015), DMI was lowered by 14% in cows with an experimental diet rich in very long-chain PUFA from fish oil, which was consistent with earlier reports (e.g., Loor et al., 2005; Gama et al., 2008; Moate et al., 2013), and had no effects on DMI in goats, as previously observed (Toral et al., 2014).

Based on the previous study of cows and goats fed fish oil at 2% DMI (Toral et al., 2015), which supplied 32.2 and 3.8 g/d of docosahexaenoic acid (**DHA**) and 77.1 and 9.1 g/d of eicosapentaenoic acid (**EPA**), respectively, the MAP treatment, with a higher DHA intake (115.5 and 13.4 g/d in cows and goats, respectively; Table 2) and a lower level of EPA (1.1 and 0.1 g/d), was chosen to test the hypothesis of the effect of DHA alone. The MAP decreased milk fat content in cows by 22% and in goats by 15%, relative to the control, which was in line with data from Toral et al. (2015) in goats and cows fed fish oil. However, previous indirect comparison studies (Offer et al., 1999; Shingfield et al., 2003; Gagliostro et al., 2006; Gama et al., 2008; Toral et al., 2014) showed that fish oil results in differences in milk fat synthesis in cows (decrease) and goats (no effect). These differences in milk fat responses to fish oil between the study by Toral et al. (2015) and earlier investigations in goats (Gagliostro et al., 2006; Toral et al., 2014) had been attributed to a higher intake of EPA plus DHA in the former, 0.58 versus 0.12 to 0.28% DM, respectively. However, in the present study, the supply of EPA was very low (Table 2), and the intake of DHA from MAP was approximately 0.55% DM, similar to the intake of EPA plus DHA under the fish oil treatment in Toral et al. (2015). Moreover, we found a similar effect of MAP and fish oil treatment, which supplied similar amounts of either DHA or EPA

plus DHA (Toral et al., 2015), on milk fat in goats and cows, which implied similar effects of DHA alone or DHA combined with EPA.

The MAP treatment resulted in significant increases in numerous 20- to 22-carbon chain FA, particularly 20:5n-3, 22:5n-3 and 22:6n-3 [EPA, docosapentaenoic acid, and DHA] in both species, with greater increases in cows, whereas 20:3n-3, 20:4n-6, 22:4n-6 specifically increased in cows (Table 8). The average estimated transfer efficiency of supplemental DHA into milk among species with MAP (9.6%) was higher to than that from fish oil treatment (4.7% in Toral et al., 2015) and similar to the results of Franklin et al. (1999) in cows (8.4% for unprotected algae). The MAP treatment specifically increased *trans*-4 and *trans*-13 18:1 isomers in cow milk (Table 4), which agreed with the specific BH pathway adaptations in response to dietary conditions among species.

The addition of fish oil or marine algae rich in long-chain PUFA to the diet is known to inhibit the complete biohydrogenation of C18 UFA, resulting in increased outflow of ruminal *trans* 18:1 and *trans* 18:2 isomers (Shingfield et al., 2010). Consequently, ruminal *trans* 18:1 increased and 18:0 synthesis decreased under these conditions. In both species, MAP induced increases in *trans*-18:1 and similar decreases in the sum of 18:0 and *cis*-9 18:1 in milk (by a mean of 60%; Table 3), in line with lower 18:0 outputs from the rumen being available for absorption and mammary gland uptake. Compared with the previous study by Toral et al. (2015) using fish oil treatment, similar effects on 18:0 and *cis*-9 18:1 were observed in goats and cows in the present study. Indeed, this treatment in Toral et al. (2015) decreased 18:0 and *cis*-9 18:1 by 69 and 55%, respectively, in cows [versus -61% (Table 3) and -57% (Table 4) in the present study], whereas the sum of *trans*-FA increased by 334% (versus 212% in the present study). Similarly, in goats fed 2% DM of fish oil (Toral et al., 2015), 18:0 and *cis*-9 18:1 decreased by 79 and 69%, respectively (versus -68 and -58% in the present study), whereas the sum of *trans*-FA increased by 270% (versus 164% in the present study). The smallest effect on the sum of *trans*-FA in the present study compared with that in Toral et al. (2015) could be due to differences in the nature and composition of the marine supplements, particularly the higher dietary DHA content in MAP compared with fish oil.

Therefore, it was proposed that the negative effect of marine lipids rich in long-chain FA on milk fat synthesis occurs via a decrease in ruminal 18:0 outflow accompanied by collective increases in *trans*-FA that cannot be desaturated by stearoyl-CoA desaturase (**SCD**) in the ruminant mammary gland, which increases the mean melting point and decreases the milk fat fluid-

Table 8. Effect of dietary supplements of corn oil and starch or marine algae powder or hydrogenated palm oil on milk 20- and 22-carbon fatty acids (FA) in cows and goats¹

FA, g/100 g of FA	Cows				Goats				SEM	<i>P</i> -value ²		
	Control	COS	MAP	HPO	Control	COS	MAP	HPO		Sp	D	Sp × D
20:0	0.14 ^{bc}	0.11 ^{cd}	0.11 ^d	0.14 ^{bc}	0.14 ^{bc}	0.17 ^a	0.11 ^d	0.15 ^b	0.0043	0.008	<0.001	<0.001
<i>cis</i> -9 20:1	0.11 ^a	0.12 ^a	0.076 ^b	0.11 ^a	0.015 ^c	0.019 ^c	0.022 ^c	0.018 ^c	0.0045	<0.001	0.010	0.001
<i>cis</i> -11 20:1	0.024 ^d	0.097 ^a	0.060 ^b	0.021 ^d	0.034 ^{cd}	0.054 ^b	0.046 ^{bc}	0.028 ^{cd}	0.0025	0.012	<0.001	<0.001
20:2n-6	0.043	0.034	0.038	0.042	0.019	0.019	0.025	0.019	0.0016	<0.001	0.293	0.197
20:3n-6	0.071	0.047	0.076	0.068	0.023	0.021	0.036	0.022	0.0022	<0.001	<0.001	0.066
20:3n-3 ³	0.018 ^b	0.019 ^b	0.051 ^a	0.018 ^b	0.018 ^b	0.014 ^b	0.019 ^b	0.015 ^b	0.0015	<0.001	<0.001	<0.001
20:4n-6	0.12 ^{bc}	0.074 ^d	0.30 ^a	0.11 ^{cd}	0.15 ^b	0.15 ^{bc}	0.26 ^a	0.13 ^{bc}	0.0058	0.013	<0.001	<0.001
20:5n-3	0.072 ^c	0.035 ^c	0.36 ^a	0.063 ^c	0.052 ^c	0.047 ^c	0.15 ^b	0.048 ^c	0.0067	<0.001	<0.001	<0.001
22:0	0.058 ^a	0.022 ^c	1.15 ^{abc}	0.053 ^{ab}	0.041 ^{bcd}	0.033 ^{de}	0.041 ^{bcd}	0.038 ^{cd}	0.0020	0.010	<0.001	<0.001
22:2n-6	0.038 ^b	0.013 ^b	0.13 ^a	0.038 ^b	0.000 ^b	0.002 ^b	0.023 ^b	0.000 ^b	0.0055	<0.001	<0.001	<0.001
22:4n-6	0.016	0.025	0.037	0.018	0.016	0.018	0.029	0.013	0.0020	0.095	<0.001	0.675
22:5n-3 ⁴	0.11 ^c	0.072 ^c	0.29 ^a	0.10 ^c	0.10 ^c	0.090 ^c	0.18 ^b	0.092 ^c	0.0075	0.011	<0.001	<0.001
22:6n-3	0.074 ^c	0.040 ^c	1.15 ^a	0.069 ^c	0.078 ^c	0.10 ^c	0.77 ^b	0.083 ^c	0.028	0.079	<0.001	<0.001
24:0	0.037 ^a	0.015 ^b	0.040 ^a	0.035 ^a	0.014 ^b	0.016 ^b	0.020 ^b	0.016 ^b	0.0014	<0.001	<0.001	<0.001
24:1n-5 ⁵	0.014	0.043	0.028	0.012	0.010	0.017	0.016	0.008	0.0032	0.020	0.005	0.206

^{a-e}Means within a row not sharing a common superscript differ ($P < 0.05$) due to species by diet interactions.

¹Control = basal diet containing no additional oil; COS = basal diet containing corn oil and wheat starch; MAP = basal diet containing marine algae powder; HPO = basal diet containing hydrogenated palm oil.

²Probability of significant effects due to species (Sp), experimental diet (D), and their interaction (Sp × D).

³Coelutes with *cis*-13 22:1.

⁴Coelutes with 26:0.

⁵Coelutes with 22:3n-3.

ity (Loor and Herbein, 2003; Loor et al., 2005; Gama et al., 2008). Otherwise, under these conditions the increase in *trans*-11 18:1 output from the rumen lead to increases *cis*-9,*trans*-11 CLA in milk (Tables 4 and 5). However, the delta-9 desaturation ratios, which are commonly used as estimators of SCD activity (Bernard et al., 2013), are marginally modified under this treatment (Table 3), suggesting an absence of compensation mechanisms via SCD activity.

Conversely, a recent study in dairy ewes (Toral et al., 2018) showed that the addition of 18:0 in the diet does not correct the MFD induced by fish oil, suggesting that other mechanisms in addition to the decrease in ruminal production of 18:0 may be involved. It remains possible that specific intermediates formed during the metabolism of dietary PUFA constituents, in addition to the dietary long-chain PUFA, may also contribute to MFD in animals fed diets containing marine lipids (Shingfield and Griinari, 2007; Bernard et al., 2008). In addition, increases in *trans*-7,*cis*-9 CLA and *trans*-9,*trans*-11 CLA in cows fed MAP were negatively associated with milk fat content ($r = -0.705$, $n = 24$, $P < 0.001$ and $r = -0.606$, $n = 24$, $P < 0.01$, respectively), as observed in cows fed COS. Additionally, it may be noted that, with MAP (in the present study) and fish oil supplementation (Toral et al., 2015), the abundance of *trans*-10,*cis*-12 CLA was not altered in either species, which is consistent with earlier studies showing that

an increase in the milk *trans*-10,*cis*-12 CLA concentration (Loor et al., 2005; Shingfield and Griinari, 2007; Toral et al., 2014) or a greater accumulation of *trans*-10,*cis*-12 CLA in the rumen (Shingfield and Griinari, 2007; Boeckeaert et al., 2008) is uncommon in ruminants fed marine lipids, even though MFD is always observed at least in cows.

Response to Hydrogenated Palm Oil

Previous research on dairy cows has reported different effects of saturated fat supplementation on DMI and milk production parameters. In the present study, HPO (containing 47% of 16:0 and 48% of 18:0, supplying 1.3 and 1.4% DM of 16:0 and 18:0, respectively, representing a 6-fold increase in C16:0 and a 38-fold increase in C18:0 in both species; Table 2) had no adverse effects on milk yield and DMI in both species. This was in contrast to the 7 to 10% decrease in DMI reported in cows (Rico et al., 2014) fed a diet supplemented with high-palmitic acid (containing 84.8% of 16:0 and 8.3% of 18:1, supplying 2.1 and 1% DM, respectively). This result is consistent with previous reports showing that long-chain SFA supplements usually have little effect on DMI compared with UFA supplements (Allen, 2000).

In cows, HPO induced a 13% increase in milk fat content compared with the CTL (Table 2), which agrees (Mosley et al., 2007; Piantoni et al., 2013) with

the results of other studies of cows fed palmitic acid-supplemented diets, with the exception of Rico et al. (2014).

No positive effect of palm oil supplementation on milk fat content was observed in goats (with a slight increase by 4%; Table 2). As expected, enrichment of 16-carbon FA in cow milk was observed that specifically resulted from an increase in 16:0 (Table 3), but not in goats. This observation in cows was accompanied by a decrease in the sum of <C16 FA yield (Figure 1), synthesized *de novo*, as observed in other experiments with palmitic acid-enriched dietary treatments (Piantoni et al., 2013), but other studies reported large increases in 16:0 yield without a decrease in *de novo* FA yield (Mosley et al., 2007). Conversely, HPO does not alter the milk FA profile in goats, except for a specific decrease in 10:0. Again, these data highlighted interspecies-specific responses to lipid supplements, particularly 16:0- and 18:0-enriched supplements. These differences likely originate from intermediary (availability of FA) and mammary (uptake of FA) metabolism due to the moderate effect of these SFA-enriched supplements on milk *trans* FA.

Milk LPL Activity

In recent decades, research showed that, in addition to milk FA secretion, milk LPL activity and fat lipolysis responses to nutritional factors also differ markedly between goats and cows (Chilliard et al., 2014). Regardless of diet, LPL activity was higher in cows than in goats (means of 498 and 396 nmol/mL, respectively; Table 2), in line with the results of earlier studies (Toral et al., 2015; Chilliard et al., 2003; Chilliard et al., 2014). However, in both species, the milk LPL activity was decreased to a similar extent with lipid supplements, except for MAP, which did not significantly reduce LPL activity in goats compared with the CTL. Previous studies in goats demonstrated that dietary plant oil and oilseed or fish oil supplements decreased milk LPL activity (Eknæs et al., 2009; Chilliard et al., 2014), and Toral et al. (2015) suggested the existence of a dose-dependent relationship with LPL activity with fish oil treatment. The decrease in LPL activity in cows fed the 3 lipid supplements is consistent with the result obtained for fish oil in the earlier study (Toral et al., 2015).

CONCLUSIONS

A direct comparison of the milk fat content and yield responses to various diets that were either rich in

starch and supplemented with corn oil or supplemented with marine algae or hydrogenated palm oil supports species-specific regulation of ruminal and postabsorptive tissue metabolism. In particular, COS caused a shift from the *trans*-11 to the *trans*-10 pathway in the rumen in cows, which was far less pronounced in goats. However, it is likely that other BH intermediates (*trans*-7,*cis*-9 CLA, *trans*-9,*trans*-11 CLA, and *trans*-10,*trans*-12 CLA) with antilipogenic effects may intervene to explain MFD with COS as well as other mechanisms, such as the observed decrease in plasmatic precursors of the *de novo* FA synthesis (acetate and BHB), which probably contributes to a reduction in milk fat synthesis in this species. Supplements of DHA-rich marine algae resulted in similar responses among species inducing MFD, although to a lesser extent in goats than in cows. In both species, changes in the milk FA composition were characterized by decreases in 18:0 and *cis*-9 18:1, increases in *trans*-18:1 and $\geq$ C20, and no effect on *trans*-10,*cis*-12 CLA. The HPO treatment increased the milk fat content in cows, but not in goats, and was accompanied by an increase in 16-carbon FA in the milk of this species, suggesting that cows had a greater ability to incorporate C16:0 in milk fat than goats, probably due to differences in postabsorptive tissue metabolism. These data confirm the hypothesis of a greater stability of the caprine milk fat content and secretion response to dietary conditions that either decrease or increase milk fat content and yield in cows. The in-depth analysis at the level of rumen, intermediary, and mammary gland metabolism of the present study will offer an efficient means to decipher the underlying mechanisms. These data will contribute to the development of feeding strategies to alter the milk FA composition and optimize milk fat production.

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