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Milk fat depression and plasma lipids in dairy cows and goats

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ABSTRACT

This study examines the effects of diets supplemented with various lipids selected to induce divergent milk fat content responses (including a milk fat depression) between dairy cows and goats on plasma lipid composition. The objective was to better understand the mechanisms behind the regulation of milk fat secretion in these two ruminant species. Twelve Holstein cows and 12 Alpine goats were fed a basal diet not supplemented (CTL) or supplemented with corn oil plus wheat starch (**COS**, 5% DM intake (DMI)), marine algae powder of *Schizochytrium sp.* (**MAP**, 1.5% DMI), or hydrogenated palm oil (**HPO**, 3% DMI), in a replicated 4 × 4 Latin square design, during 28 days. On day 27, blood samples were collected for lipid analysis. Plasma lipid classes were quantified by high-performance thin-layer chromatography, with triacylglycerol (**TAG**) and free fatty acid (**FFA**) fractions analysed for FA composition by GLC. Plasma molecular species of TAG and ceramides were determined by HPLC–high-resolution MS and by liquid chromatography–triple quadrupole, respectively. Irrespective of diet, plasma total lipid content was higher in cows than goats (+61%), and TAG concentration was higher in goats than cows (+157%). In cows, conversely to goats, COS increased the *trans*-10 C18:1 proportion in the free FA (+248%) and the TAG (+195%) fractions. In cows and goats, MAP induced increases in cholesterol esters, cholesterol and phospholipids compared to CTL and changes in the plasma free FA and FA of TAG profiles. In both ruminant species, the concentrations of the lipid fractions were unchanged by HPO compared to CTL. Our results point to species specificities and different diet effects in plasma concentrations and compositions of lipid fractions in cows and goats. These new data highlight how diets, that induce large variations in milk fat secretions, affect the plasma lipid classes available for milk fat synthesis.

Implications

A direct comparative study between lactating cows and goats was performed to test the hypothesis that plasma lipid classes are differentially modulated by diets supplemented with various lipids affecting milk fat concentration and that the fatty acid composition of plasma lipid classes varies between animal species. The results showed major inter-species differences in plasma neutral and polar lipid composition in response to dietary lipids and highlighted plasma lipid molecules associated with milk fat depression. Species- and diet-dependent variations in plasma lipid class compositions offer clues to help decipher the underlying mechanisms controlling milk fat plasticity.

Introduction

The composition and concentration of the milk lipid fraction are among the determinants of the nutritional quality of dairy products for consumers and the efficiency of milk production for producers. Feeding is an efficient, rapid and reversible means to modulate the production and composition of milk fat, in particular through the addition of lipids in the diet, which were first used to increase the energy value of the rations and later to improve the nutritional quality of milk (Chilliard et al., 2007). However, polyunsaturated fatty acid (**PUFA**)-rich plant products added to starch-rich diets or marine-source products added as feed supplements typically lead to a reduction in milk fat concentration known as milk fat depression (**MFD**) in dairy cows (Bauman and Griinari, 2003, 2001) but not—or to a lesser extent—in goats (Toral et al., 2015). This MFD has been attributed, at first, to dietary PUFA inducing a shift in ruminal biohydrogenation leading to the formation of *trans*-10 intermediates, C18:1 and C18:2 with potential or demonstrated antilipogenic effects (Bauman et al., 2011). In partic-

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ular, *trans*-10, *cis*-12 conjugated linoleic acid plays a role in decreasing milk fat synthesis in dairy cows (Baumgard et al., 2000) and goats when used at higher doses (Lock et al., 2008; Shingfield et al., 2009), in part by down-regulating mammary lipogenic gene expression (Shingfield et al., 2010). However, other ruminal biohydrogenation intermediates and mechanisms may be involved. The specific regulations of lipid metabolism in the rumen (Toral et al., 2016), adipose tissue (Harvatine et al., 2009) and mammary gland (Bernard et al., 2017) to diet-induced MFD according to diet composition and animal species have been investigated and reviewed (Shingfield et al., 2010) whereas only one study reports plasma lipid concentrations and composition under those conditions (Delavaud et al., 2019). However, to better understand the mechanisms underlying MFD, it is essential to characterize specifically the triacylglycerols (**TAGs**) and free fatty acid (**FFA**) plasma lipid fractions whose fatty acids (**FAs**) are taken up by the mammary gland and used for milk fat synthesis. Thus, milk FAs esterified on TAG have two origins: (1) the *de novo* synthesis by mammary epithelial cells and (2) the mammary uptake of the circulating FA in the form of free FA or TAG in chylomicrons or very-low-density lipoproteins. These two pathways give rise to the formation of (1) short- and medium-chain FA (4:0–16:0) representing 40% of the milk FA, and (2) long-chain FA (≥C16) representing 60% of milk FA (Bernard et al., 2018). Indeed, the differences between species in FA transport and resulting mammary absorption, including those that may exert an antilipogenic effect, could explain differences in milk fat yield. Moreover, the addition of lipids to ruminant diets increased circulating phospholipid (**PL**) and cholesterol esters that contribute to variations in lipid metabolism by modulating the circulating high-, low- and very-low-density lipoproteins differentially used by tissues. More recently, the plasma ceramides have emerged as molecules potentially involved in nutrient partitioning and lactation physiology (Davis et al., 2021; McFadden and Rico, 2019). Furthermore, ceramide synthesis may be modulated by the nutrition of the animals, with dietary palmitic acid supply being shown to increase circulating ceramides and milk yield (Rico et al., 2016) while PUFA, compared to saturated FA consumption, decreased ceramide accumulation in rat skeletal muscle (Blachnio-Zabielska et al., 2010). Taken together, these data suggest that nutritional regulation of milk composition may be associated to alteration in circulating ceramides via their involvement in modulating insulin signalling and nutrient partitioning.

This work is part of a comparative study between dairy cows and goats under strictly similar dietary conditions with the same basal diet either supplemented in corn oil and supplemental starch (**COS**), or marine algae powder of *Schizochytrium sp*. (**MAP**), or hydrogenated palm oil (**HPO**) compared to non-lipid-supplemented control. These treatments were chosen for their contrasted and divergent effects on MFD according to ruminant species, by either decrease or increase of milk fat secretion (Fougère et al., 2018). We have already investigated and reported the effects of these diets on milk TAG and polar lipid profiles (Fougère et al., 2021), mammary lipid metabolism (Fougère and Bernard, 2019) and ruminal digestive parameters (Martin et al., 2021).

The objective of this study was to characterize plasma lipid composition in cows and goats in response to lipid supplementation from the same experiment (Fougère et al., 2018). Plasma lipid class content and composition were determined focusing on TAG and FFA fractions available for mammary uptake and on ceramides.

We hypothesized that (i) the concentration of the plasma TAG and FFA and their FA profiles would differ among species and dietary treatments and that these profiles would be richer in FA with antilipogenic effect in cows and goats that experienced MFD, (ii) the plasma of cows and goats receiving PUFA-rich lipid supplements would be richer in PL and cholesterol ester fractions, and (iii) that ceramides would be decreased by dietary treatments rich in PUFA (COS and MAP) and increased with the FA saturated-rich treatment (HPO) at least in cows for which strong variations in milk fat yield were observed with these treatments. The final aim was to provide new elements in the divergent responses between these two ruminant species to diet-induced MFD.

Material and methods

Animals, experimental design, diets, and management

Details of the experimental design can be found in Fougère et al. (2018). Briefly, 12 Holstein cows and 12 Alpine goats, all multiparous and non-pregnant, at 86 ± 24.9 and 61 ± 1.8 days in milk, respectively, were allocated to one of four groups in each species (three animals per group, balanced according to days in milk, milk yield, milk fat, and milk protein content) and randomly assigned to treatments in a replicated 4 × 4 Latin square design with 28-d experimental periods. Treatments were *ad libitum* intake of diets composed of long grass hay (first cycle from natural permanent half mountain grassland) and concentrate containing either no additional lipid (control, **CTL**), corn oil (5.0% of total DM intake (**DMI**)) and wheat starch (**COS**), marine algae powder of *Schizochytrium sp*. (MAP, 1.5% of total DMI), or hydrogenated palm oil (HPO, 3.0% of total DMI) (Table 1). Diets were offered as two equal meals at 0830 h and 1600 h. Concentrate and hay refusals were weighed daily and used to adjust the amounts of feed offered to maintain the targeted dietary forage-to-concentrate ratio (45:55 on a DM basis). The animals had *ad libitum* access to fresh water and were milked at 0800 h and 1500 h.

Measurements and sample collection

Feed intakes were recorded daily on the last week of each experimental period. For each species, hay and concentrates were collected weekly during the last 3 weeks of each 28-day experimental period at a rate of one sample per week and pooled to be representative of the period. For each species, four samples of hay and four samples of concentrate were used to determine chemical composition as presented in Table 1 (Association of Official Analytical Chemists (AOAC) International, 2005) and performed as previously detailed (Fougère et al., 2018; Martin et al., 2021). The milk yields of individual animals were recorded over six milkings on days 21, 22 and 24 of each experimental period. Simultaneously, individual milk samples were collected with preservative (bronopol-B2; LIAL, Aurillac, France) for chemical analyses performed as previously described (Fougère et al., 2018). Blood samples were collected before the morning milking on day 27 of each experimental period on all animals from the jugular vein into evacuated collection tubes containing ethylenediaminetetraacetic acid (**EDTA**, 9 ml, Terumo Vacutainer-LML, Nemours, France). Immediately after collection, the blood was centrifuged (1 100*g*, 15 min, 4 °C), and the plasma was stored at −80 °C before targeted lipid and semi-targeted lipidomic analyses (Fig. 1).

Plasma lipid analysis

Lipid class concentrations were analysed by High-Performance Thin-Layer Chromatography. Total lipids in plasma were extracted by a slightly modified Folch et al. (1957) procedure. Chemicals were purchased from Sigma–Aldrich (Darmstadt, Germany) and Honeywell (Seelze, Germany). Briefly, lipids were extracted from 500 µl by addition of chloroform/methanol (1/1, vol/vol, 6 ml).

Table 1
Ingredients and chemical composition of the basal concentrates offered to cows and goats either without lipid supplementation (CTL) or supplemented with corn oil and starch (COS), marine algae powder of *Schizochytrium sp.* (MAP) or hydrogenated palm oil (HPO), and of the grassland hay. Source Fougère et al. (2018).

	Concentrate				Forage
Item	CTL	COS	MAP	HPO	Grassland Hay
Ingredients, g/kg of DM					
Wheat starch	.	395	.	.	.
Corn	532	394	518	500	.
Soy	138	150	142	147	.
Dehydrated Alfalfa	275	.	283	294	.
Molasse 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	.
Corn Oil	.	50	.	.	.
Marine algae powder	.	.	15	.	.
Hydrogenated palm oil	.	.	.	30	.
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
Fatty acids, g/kg of DM					
C14:0	0.04	0.02	0.4	0.24	0.07
C16:0	3.91	5.87	4.05	10.9	2.38
C18:0	0.62	0.78	0.59	8.33	0.20
cis-9 C18:1	5.43	12.0	3.98	4.44	0.35
C18:2n-6	12.6	24.8	8.7	9.7	1.98
C18:3n-3	2.01	0.82	2.84	1.62	4.98
C22:6n-3	ND	ND	3.06	ND	0.004
Energy, MJ/kg of DM[1]	6.43	7.66	6.51	6.82	4.84
Protein, g PDI /kg of DM[2]	102	104	103	103	55

Abbreviations: OM = organic matter; MJ = mega Joule; PDI = protein digestible in intestine.
[1] Net energy for lactation calculated according to INRA (2007).
[2] PDI (protein digestible in the intestine) calculated according to INRA (2007).

After vortex and centrifugation (1 500*g*, 10 min, +10 °C), the top layer was transferred into a clean glass tube and 3 ml of chloroform and 1.8 ml of acidic NaCl (17 mM, H_2SO_4, 1 mM, 1‰) were added. After vortex and centrifugation (1 500*g*, 10 min, 10 °C), the organic layer containing lipids was collected, dried under N_2, and dissolved into chloroform and held at −20 °C. The 96 samples of lipid extracts, corresponding to the 12 cows and 12 goats in each of the four treatment periods (12 × 4 = 48 per species), were analysed by High-Performance Thin-Layer Chromatography (Camag, Switzerland) for lipid classes separation and quantification (Supplementary Material S1). Briefly, the total lipid extracts were randomly distributed across the plates on which a mix of standards of cholesterol esters, TAG, FFA, cholesterol, and PL was deposited. After development and derivatization, the concentrations of lipid classes were determined using their respective standard curve and expressed in mg/dl of plasma (Supplementary Table S1).

After High-Performance Thin-Layer Chromatography separation, the free and TAG FA profiles were determined by GLC as previously described (Delavaud et al., 2019). Individual plasma samples of the same group were pooled by period and diet for each ruminant species (three animals per period and dietary treatment) using equivalent volumes to finally obtain 16 samples (four diets × four periods) per species. The total lipids were extracted as described above, with addition of 4.5 µg of *trans*-9, *trans*-11 conjugated linoleic acid (1181, Matreya LLC, State College, PA) and 5.4 µg of trilaurin (T7140, Sigma–Aldrich) as qualitative internal standards for the extraction and methylation steps, then deposited on plates in large volumes by area spray. The bands corresponding to TAG and FFA were scraped off and extracted from the silica as previously described (Delavaud et al., 2019). The lipids were transmethylated, and FA methyl esters were analysed by GLC using a 100 m fused silica capillary column (CP-SIL88; Chrompack 7489, Middelburg, The Netherlands) in a Perichrom 2100 system equipped with a flame-ionization detector (Perichrom, Saulx-les-Chartreux, France) as previously described (Delavaud et al., 2019). The free and TAG FA profiles were expressed as relative abundance to the total FA analysed.

The molecular species of TAG (C:n) and ceramides were analysed by HPLC–High-Resolution MS and Liquid Chromatography–triple quadrupole, respectively. These semi-targeted lipidomic analyses were performed on the Metatoul-Lipidomics Platform (Inserm UMR1048, Toulouse, France) which is certified to ISO 9001:2015 standards. Individual plasma samples were pooled by period and diet to finally obtain 16 plasma samples for each species, cows or goats. Then, 10 µl of each pooled plasma sample was spiked with 2 µg of TAG (19:0/19:0/19:0, Sigma Aldrich, France) as internal standard. For further analysis of ceramides, 20 µl of plasma was spiked with 16 ng of ceramide d18:1–15:0 (Avanti Polar Lipids, AL) as internal standard. Then, for all further analysis, total plasma lipids were extracted according to Bligh and Dyer (1959), and molecular species of TAG and ceramides were analysed as detailed in Fougère et al. (2021). For each TAG (C:n) species, the analytical area was normalized by area of internal standard and expressed as percent of total area of TAG analysed, where C = number of non-glycerol-backbone carbons and n = number of double bonds. Molecular species of ceramides were expressed in relative abundances to the internal standard: area of sample × internal standard (ng) / area of internal standard / plasma volume (ml).

Statistical analysis

All the data were tested by ANOVA for a 4 × 4 Latin square design using the mixed procedure of SAS 9.4 statistical software (SAS, 1988). The statistical model included period (1, 2, 3 and 4),

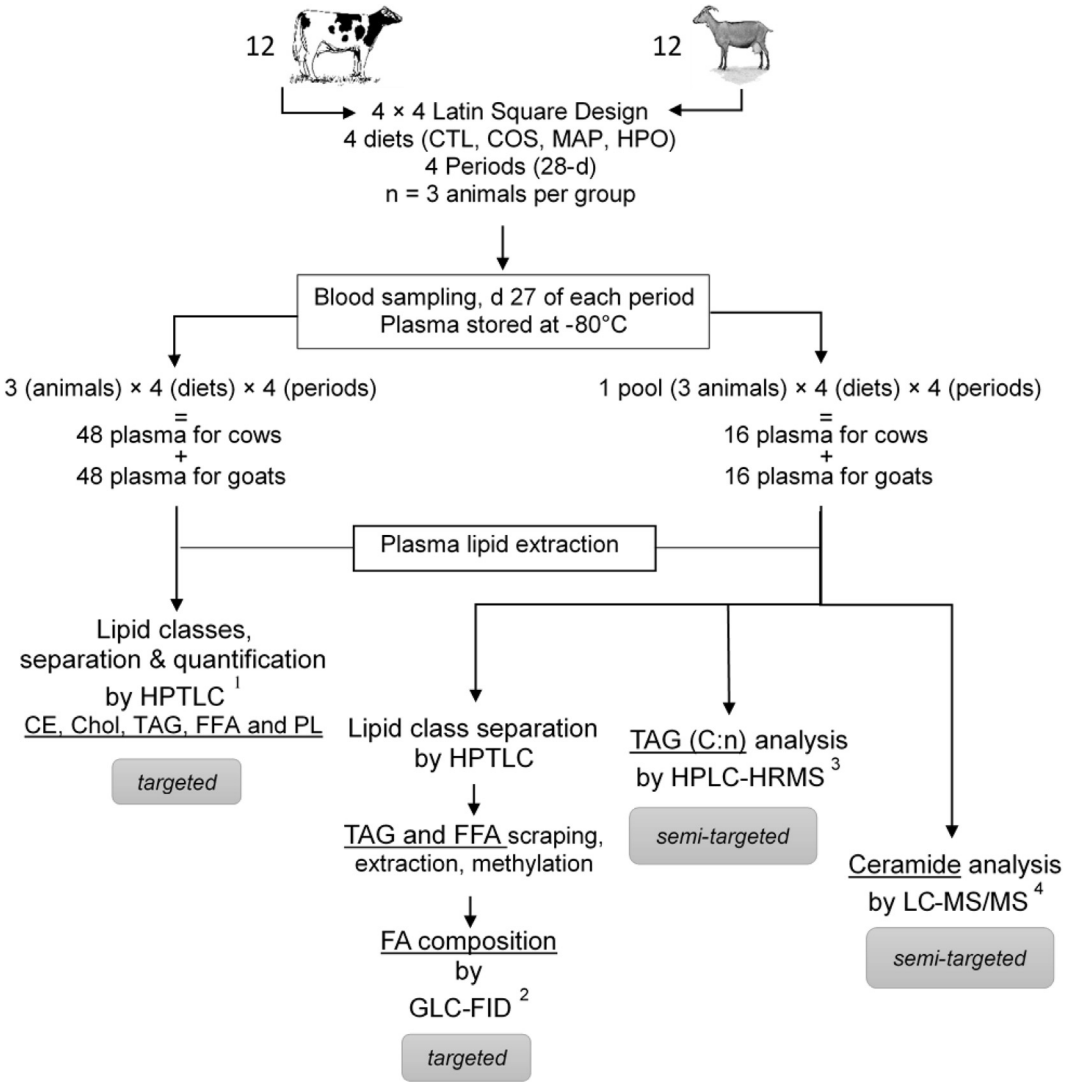

Fig. 1. Schematic representation of targeted and semi-targeted plasma lipidomic analyses made in plasma of cows and goats fed control diet (CTL) or lipid-supplemented diets with corn oil and starch (COS, 5% DM intake (DMI)), marine algae powder of *Schizochytrium sp.* (MAP, 1.5% DMI) or hydrogenated palm oil (HPO, 3% DMI).;[1]High-performance thin-layer chromatography; [2]GLC–flame-ionization detector; [3]HPLC–high-resolution MS; [4]Liquid chromatography–MS.

species (cow and goat), diet (CTL, COS, MAP and HPO), and species × diet interaction as fixed effects. For lipid class analyses, animals in groups (i.e. the three cows or three goats allocated to the same diet for each of the four periods) were included as random effects. For analysis performed on samples composed of the three animals on the same diet during the same period (FA analysed by GLC; TAG and ceramides analysed by LC–MS), the group was included as random effect. The normality of data distribution was tested (Shapiro–Wilk, Kolmogorov-Smirnov, Cramer-von Mises, and Anderson-Darling tests), and the data were log-transformed and re-analysed in case of significance ($P < 0.05$). The KENWARD-ROGER option was used, and least square means (LSMEANS) were compared using a Tukey-Kramer-adjusted PDIFF. Differences were declared significant at a *P*-value < 0.05. Pearson correlation coefficients were calculated for associations between abundances of molecular species of TAG (C:n) and FA of TAG analysed by GLC.

Results

Intake, performances and production parameters of cows and goats are presented in Table 2 and were previously detailed in Fougère et al. (2018). In cows, milk fat concentration decreased with COS and MAP (−45% and −22%, respectively) but increased with HPO (+13%). In goats, only MAP decreased milk fat concentration (−15%) whereas no effect was observed with COS and HPO.

Plasma concentrations in lipid classes

Individual concentrations of cholesterol esters, cholesterol, PL, TAG and FFA, and their sum (total lipids) of cows and goats fed the CTL, COS, MAP and HPO diets are presented in Table 3. On the CTL diet, cow plasma compared with goat plasma contained 61% more total lipids ($P < 0.001$), higher concentrations of cholesterol esters (+100%, $P < 0.001$) and cholesterol (+73%, $P = 0.003$). In contrast, goat plasma contained 157% more TAG ($P < 0.001$) than cow plasma. The COS diet increased plasma total lipids (+38%, $P = 0.007$) and cholesterol (+47%, $P = 0.016$) in goats, and PL (+23%, $P = 0.0003$) in cows and goats, compared to CTL. Regardless of species, the MAP diet increased plasma total lipids (+41%, $P < 0.0001$), cholesterol esters (+58%, $P < 0.0001$), cholesterol (+51%, $P < 0.0001$) and PL (+22%, $P = 0.0002$) compared to CTL. In both cows and goats, the HPO diet did not change plasma concentrations of lipid classes compared to CTL.

Table 2
Intake, performance and production parameters of cows and goats fed diets without lipid supplementation (CTL, $n = 12$) or supplemented with corn oil and starch (COS, $n = 12$), marine algae powder of *Schizochytrium sp.* (MAP, $n = 12$) or hydrogenated palm oil (HPO, $n = 12$). Adapted from Fougère et al. (2018).

	Cows				Goats				SEM	Statistical effects, *P*-values[1]		
Items	CTL	COS	MAP	HPO	CTL	COS	MAP	HPO		Species	Diet	Species × Diet
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}	0.20	<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}	0.20	<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}	0.39	<0.001	<0.001	<0.001
Fatty acids, g/d												
C14:0	1.2 ^{cd}	1.0^{d}	14.5^{a}	9.0^{b}	0.1^{e}	0.1^{e}	1.7^{c}	1.1^{d}	0.07	<0.001	<0.001	<0.001
C16:0	64.2^{d}	151^{b}	96.3^{c}	353^{a}	7.4 ^{g}	19.0^{f}	11.2 ^{g}	43.0^{e}	1.76	<0.001	<0.001	<0.001
cis-9-C16:1	0.5^{c}	1.2^{a}	0.9^{b}	0.4^{c}	0.06^{f}	0.14^{d}	0.11^{e}	0.05^{f}	0.01	<0.001	<0.001	<0.001
C18:0	8.3 ^{cd}	20.0^{c}	9.4 ^{cd}	307^{a}	1.0^{d}	2.7^{d}	1.1^{d}	37.2^{b}	1.43	<0.001	<0.001	<0.001
cis-9 C18:1	57.3^{b}	312^{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
cis-11 C18:1	2.8^{b}	8.1^{a}	3.3^{b}	2.9^{b}	0.3^{d}	1.0^{c}	0.4^{d}	0.4^{d}	0.04	<0.001	<0.001	<0.001
cis-9, *cis*-12 C18:2	146^{b}	605^{a}	120^{b}	128^{b}	17.2^{d}	75.1^{c}	14.1^{d}	16.3^{d}	2.76	<0.001	<0.001	<0.001
C18:3*n-3*	74.4^{ab}	56.6^{c}	84.0^{a}	70.0^{b}	8.2^{de}	6.8^{e}	9.7^{d}	8.5^{de}	0.72	<0.001	<0.001	<0.001
C20:5*n-3*	ND	ND	1.1	2.26	ND	ND	0.13	0.27	0.47	<0.001	-	-
C22:5*n-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}	0.02	<0.001	<0.001	<0.001
C22:6n-3	0.05^{c}	0.5^{c}	115^{a}	0.04^{c}	0.01^{c}	0.07^{c}	13.4^{b}	0.01^{c}	0.42	<0.001	<0.001	<0.001
Total	401^{d}	1 206^{a}	603^{c}	996^{b}	46.3 ^{h}	150^{e}	70.1 ^{g}	122^{f}	7.26	<0.001	<0.001	<0.001
BW, kg	678	686	678	676	54	53	54	54	11.3	<0.001	0.227	0.158
Milk yield, kg/d	27.8	25.0	26.5	27.1	3.1	3.0	2.9	3.0	0.69	<0.001	0.102	0.113
Milk fat yield, 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
Milk fat concentration, g/100 g	3.39^{bc}	1.85^{e}	2.64^{d}	3.82^{a}	3.47^{ab}	3.45^{ab}	2.95 ^{cd}	3.62^{ab}	0.91	0.002	<0.001	<0.001
Energy balance, %	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, %	113^{bc}	112^{bc}	126^{ab}	104^{c}	126^{ab}	105^{c}	138^{a}	131^{ab}	3.42	0.031	<0.001	<0.001

Abbreviation: ND = Not detected.
[1] $^{a–g}$ Means within a row that do not share a common superscript letter differ ($P < 0.05$) due to species × diet interactions.

Table 3
Cholesterol esters, cholesterol, phospholipids, triacylglycerols, free fatty acids and total lipid concentrations in individual plasma samples from cows and goats fed either control diet (CTL, $n = 12$) or lipid-supplemented diets with corn oil and starch (COS, $n = 12$), marine algae powder of *Schizochytrium sp.* (MAP, $n = 12$) or hydrogenated palm oil (HPO, $n = 12$).

	Cows				Goats				SEM[2]	Statistical effects, *P*-values[1]		
mg/dl plasma	CTL	COS	MAP	HPO	CTL	COS	MAP	HPO		Species	Diet	Species × Diet
Cholesterol esters	320^{bc}	359^{b}	497^{a}	375^{b}	160^{d}	229 ^{cd}	262^{c}	184^{d}	20.7	<0.001	<0.001	0.023
Cholesterol	38.0^{b}	42.6^{b}	56.8^{a}	43.1^{b}	22.0^{d}	32.4^{bc}	33.6^{b}	24.2 ^{cd}	2.80	<0.001	<0.001	0.019
Phospholipids	193^{B}	221^{A}	238^{A}	220^{AB}	143^{B}	195^{A}	170^{A}	160^{AB}	11.2	<0.001	<0.001	0.133
Triacylglycerols	7.32^{c}	9.40^{c}	6.25^{c}	9.56^{bc}	18.8^{a}	20.2^{a}	21.1^{a}	17.0^{ab}	1.68	<0.001	0.503	0.031
Free fatty acids	4.71^{AB}	7.04^{A}	5.00^{B}	4.88^{B}	8.60^{AB}	9.96^{A}	4.60^{B}	5.58^{B}	1.25	0.216[3]	<0.01[3]	0.103[3]
Total lipids	567^{bc}	640^{b}	810^{a}	652^{b}	352^{e}	486 ^{cd}	491 ^{cd}	390de	31.0	<0.001	<0.001	0.011

[1] a-e Least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to species × diet interactions. $^{A, B}$ least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to diet.
[2] for goats (COS, n 3), SEM = 21.4, 2.88, 11.6, 1.73, 1.30 and 32.1 for cholesterol esters, cholesterol, phospholipids, triacylglycerols, free fatty acids and total lipids, respectively.
[3] *P*-values from statistical analyses performed on log-10 values.

Plasma free and triacylglycerol fatty acid profiles

The free and TAG FA profiles that were determined by GLC are reported in Tables 4 and 5, respectively. The most relevant differences between cows and goats fed the CTL diet were higher sum of monounsaturated FA and higher proportion of *cis*-9 C18:1 (+101%, $P < 0.001$) in the plasma TAG fraction of goats (Table 5). The COS diet modified the FA profiles of free and TAG FA mainly in cows by increasing the sum of monounsaturated FA (+28 and + 45.3%, respectively), in particular the *trans*-9 (+230 and + 75%, respectively), *trans*-10 (+> 300% for both), and *cis*-12 C18:1 (+135 and + 94%, respectively), and by decreasing the proportion in free C16:0 (-21%, $P = 0.027$). Compared to CTL, the MAP diet increased eicosapentaenoic acid (+>300%, $P < 0.0001$), docosahexaenoic acid (+>300%, $P < 0.0001$) and the sum of *trans* C18:1 (+182%, $P < 0.0001$) in the FFA and TAG FA profiles in both ruminant species. Compared to CTL, MAP increased (+ >300%) the proportions of *trans*-9 ($P = 0.0037$) and *trans*-10 C18:1 ($P = 0.0002$) in the FA profile of TAG in cows (Table 5). The HPO diet did not change the profile in plasma FFA for both species (Table 4), but the C16:0 proportion of the TAG fraction increased by 50% ($P < 0.0001$) and 31% ($P = 0.005$) in cows and goats, respectively (Table 5).

Plasma molecular species of triacylglycerol

Among the 43 molecular species of TAG (C:n) analysed by HPLC-HRMS (Table 6) and for animals fed the CTL diet, nine TAGs were more abundant in cows than goats, seven of which were saturated between 24:0 and 51:0, whereas five polyunsaturated TAGs between 50:3 and 60:4 were more abundant in goat plasma. Compared to CTL, the proportions of polyunsaturated TAGs 52:2, 52:3, 54:2, 54:3 and 60:2 increased in cows fed COS. With MAP diet compared to CTL, the proportions of polyunsaturated TAGs 52:2, 54:3, 56:3, 58:2 and 58:3 were increased in cows, and the proportions of TAGs 46:1 and 46:2 increased in goats whereas the TAGs 44:1, 54:6 and 56:4 were increased by MAP for both cows and

Table 4
Plasma free fatty acid profile (% of total FA) in cows and goats fed either control diet (CTL, $n = 4$) or lipid-supplemented diets with corn oil and starch (COS, $n = 4$), marine algae powder of *Schizochytrium sp.* (MAP, $n = 4$) or hydrogenated palm oil (HPO, $n = 4$).

	Cows				Goats				SEM	Statistical effects, *P*-values[4]		
% of total FA	CTL	COS	MAP	HPO	CTL	COS	MAP	HPO		Species	Diet	Species × Diet
anteiso14	0.26^{AB}	0.20^{B}	0.38^{AB}	0.32^{A}	0.11^{AB}	0.27^{B}	0.34^{AB}	0.36^{A}	0.08	0.12	0.022	0.30
C14:0	1.42	1.08	1.27	1.17	1.08	0.92	1.15	1.11	0.11	0.034	0.15	0.59
iso15	0.38^{AB}	0.29^{B}	0.38^{A}	0.44^{A}	0.26^{AB}	0.24^{B}	0.36^{A}	0.29^{A}	0.03	0.002	0.025	0.18
anteiso15	0.15	0.14	0.16	0.10	0.05	0.07	0.08	0.11	0.04	0.021	0.94	0.42
C15:0	0.64^{B}	0.53^{B}	0.73^{A}	0.55^{B}	0.48^{B}	0.42^{B}	0.66^{A}	0.55^{B}	0.04	0.009	<0.001	0.23
iso16	0.39^{A}	0.26^{B}	0.34^{A}	0.38^{A}	0.26^{A}	0.22^{B}	0.31^{A}	0.28^{A}	0.03	<0.001	0.006	0.11
cis-10 C15:1	0.08	0.13	0.06	0.11	0.08	0.07	0.14	0.08	0.03	0.97	0.88	0.087
C16:0	19.5^{ab}	15.4^{c}	15.5^{c}	21.2^{a}	17.4^{bc}	16.3^{bc}	17.1^{bc}	18.5^{abc}	0.82	0.30	<0.001	0.029
iso17 + *trans*-9 C16:1[1]	1.08^{bcd}	1.03^{cd}	1.30^{ab}	0.97^{d}	1.10^{bcd}	1.02^{cd}	1.51^{a}	1.22^{bc}	0.05	0.003	<0.001	0.032
trans-11 C16:1	0.43	0.31	0.41	0.45	0.43	0.42	0.48	0.56	0.07	0.13	0.25	0.84
cis-9 C16:1 + anteiso17[2]	1.85^{A}	1.51^{B}	1.30^{B}	1.75^{AB}	1.34^{A}	1.08^{B}	1.20^{B}	1.25^{AB}	0.11	<0.001	0.009	0.18
cis-11 C16:1	0.86^{B}	0.18^{C}	1.30^{A}	0.96^{B}	0.27^{B}	0.06^{C}	0.79^{A}	0.25^{B}	0.11	<0.001	<0.001	0.068
C17:0	1.31^{A}	0.90^{B}	1.10^{A}	1.13^{A}	1.53^{A}	1.28^{B}	1.48^{A}	1.42^{A}	0.06	<0.001	<0.001	0.56
iso18	0.21^{A}	0.08^{B}	0.09^{AB}	0.21^{A}	0.27^{A}	0.18^{B}	0.24^{AB}	0.25^{A}	0.03	<0.001	0.002	0.27
cis-10 C17:1	0.41^{AB}	0.11^{B}	0.61^{A}	0.46^{AB}	0.33^{AB}	0.20^{B}	0.52^{A}	0.24^{AB}	0.12	0.40	0.027	0.65
C18:0	31.9^{A}	26.8^{A}	16.4^{B}	34.6^{A}	33.7^{A}	36.4^{A}	20.3^{B}	36.8^{A}	1.56	0.001[5]	<0.001[5]	0.12[5]
trans-9 C18:1	0.64^{c}	2.12^{a}	1.46^{ab}	0.53^{c}	0.72^{bc}	1.07^{bc}	1.42^{ab}	0.55^{c}	0.21	0.037	<0.001	0.005
trans-10 C18:1	1.69^{bc}	7.70^{a}	4.26^{ab}	1.26^{c}	1.52^{bc}	1.52^{bc}	3.48^{abc}	1.06^{c}	0.96	0.027[5]	<0.001[5]	0.012[5]
trans-11 C18:1	1.79^{B}	4.12^{AB}	4.36^{A}	1.36^{B}	2.10^{B}	3.33^{AB}	6.81^{A}	2.24^{B}	0.91	0.13[5]	<0.001[5]	0.54[5]
trans-10 / *trans*-11 C18:1	1.00	3.26	1.15	0.90	0.72	0.55	0.52	0.50	0.49	0.022	0.61	0.32[5]
trans-13 C18:1	0.31^{B}	2.22^{AB}	2.89^{A}	1.03^{B}	0.001^{B}	0.001^{AB}	1.66^{A}	0.001^{B}	0.45	0.003[5]	0.002[5]	0.46[5]
cis-9 C18:1	17.4^{A}	13.4^{A}	8.63^{B}	14.2^{A}	22.7^{A}	20.3^{A}	14.9^{B}	18.8^{A}	1.47	<0.001	<0.001	0.88
cis-11 C18:1	0.95	0.93	0.87	0.80	0.75	0.75	0.84	0.63	0.08	0.020	0.26	0.71
cis-12 C18:1	0.35^{bc}	0.82^{a}	0.29^{c}	0.34^{bc}	0.40^{bc}	0.53^{b}	0.23^{c}	0.34^{bc}	0.05	0.030	<0.001	0.007
cis-13 C18:1	0.31^{abc}	0.38^{ab}	0.40^{a}	0.23^{abcd}	0.12^{d}	0.14^{cd}	0.25^{abcd}	0.21^{bcd}	0.04	<0.001	0.043	0.054
cis-14 C18:1 + *trans*-16 C18:1[3]	0.42^{B}	0.51^{B}	0.89^{A}	0.33^{B}	0.37^{B}	0.44^{B}	0.79^{A}	0.42^{B}	0.04	0.24	<0.001	0.15
cis-15 C18:1 + C19:0[3]	0.03^{B}	0.15^{B}	0.28^{A}	0.04^{B}	0.06^{B}	0.08^{B}	0.19^{A}	0.04^{B}	0.04	0.25	<0.001	0.40
cis-9, *cis*-12 C18:2	4.61	4.69	4.39	4.59	5.41	5.08	5.02	4.94	0.25	0.007	0.62	0.78
C20:0	0.41	0.44	0.40	0.43	0.20	0.23	0.36	0.31	0.05	<0.001	0.31	0.18
cis-11 C20:1 + C18:3n-3[3]	1.31	1.08	1.25	1.27	1.36	1.19	1.43	1.43	0.10	0.068	0.08	0.88
C21:0	0.16^{AB}	0.09^{B}	0.22^{A}	0.16^{AB}	0.02^{AB}	0.02^{B}	0.09^{A}	0.06^{AB}	0.03	<0.001	0.009	0.52
C22:0	0.37^{BC}	0.26^{C}	0.52^{A}	0.40^{B}	0.16^{BC}	0.16^{C}	0.28^{A}	0.21^{B}	0.03	<0.001	<0.001	0.15
C20:3n-6	0.26^{B}	0.33^{B}	0.37^{A}	0.26^{B}	0.09^{B}	0.04^{B}	0.16^{A}	0.06^{B}	0.03	<0.001	0.007	0.17
C20:3n-3	0.11^{AB}	0.06^{B}	0.17^{A}	0.06^{B}	0.05^{AB}	0.06^{B}	0.11^{A}	0.03^{B}	0.03	0.072	0.018	0.62
C20:4n-6	0.39^{b}	0.58^{b}	1.24^{a}	0.32^{b}	0.42^{b}	0.44^{b}	0.96^{a}	0.48^{b}	0.07	0.24	<0.001	0.012
C23:0	0.73^{AB}	0.53^{B}	0.91^{A}	0.77^{AB}	0.38^{AB}	0.25^{B}	0.52^{A}	0.39^{AB}	0.10	<0.001	0.022	0.94
C22:2n-6	0.30^{B}	0.27^{B}	0.36^{A}	0.32^{AB}	0.20^{B}	0.21^{B}	0.37^{A}	0.28^{AB}	0.04	0.058	0.012	0.56
C20:5n-3	0.27^{c}	0.39^{c}	1.64^{a}	0.24^{c}	0.20^{c}	0.21^{c}	0.81^{b}	0.29^{c}	0.07	<0.001	<0.001	<0.001
C24:0	0.83^{bc}	0.59^{cd}	1.58^{a}	1.00^{b}	0.36^{d}	0.30^{d}	0.65^{bcd}	0.41^{d}	0.09	<0.001	<0.001	0.004
C22:5n-3	0.44^{bc}	0.66^{b}	1.42^{a}	0.42^{bc}	0.15^{c}	0.14^{c}	0.50^{bc}	0.29^{bc}	0.08	<0.001	<0.001	<0.001
C22:6n-3	0.65^{c}	1.02^{c}	9.53^{a}	0.54^{c}	0.57^{c}	0.66^{c}	4.11^{b}	0.69^{c}	0.35	<0.001	<0.001	<0.001

[1] In sum, Iso17 is theoretically the most abundant.
[2] In sum, *cis*-9 C16:1 is theoretically the most abundant.
[3] Impossible to say, a priori, which is the most abundant in the sum.
[4] $^{a-d}$ Least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to species × diet interactions. $^{A-C}$ least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to diet.
[5] *P*-values from statistical analyses performed on log-10 values.

goats. For HPO diet, no increase in TAG (C:n) was observed for cows or goats.

Plasma molecular species of ceramides

As shown in Table 7, all the plasma ceramide molecular species differed between cows and goats whatever the treatment diet, whereas with the CTL diet, the only difference was higher ceramide d18:1–16:0 in cows (+142%, $P = 0.002$) than in goats. The COS diet increased most of ceramides in goat's plasma (−18:0, −20:0, −22:0, −24:0, −24:1 and −26:0), whereas the d18:1–18:1 was increased for both cows and goats. The MAP diet increased unsaturated 16:1-, 24:1- and 26:1, and saturated 24:0-ceramides in both species, and increased d18:1–22:0 in cows and d18:1–26:0 in goats. No variation in plasma ceramides was observed in response to HPO whatever the animal species.

Discussion

Plasma lipid composition is different between cows and goats with control diet

Few results from direct comparisons in plasma lipids between cows and goats, fed the same diet, were reported in the literature. The higher plasma total lipids, cholesterol esters and cholesterol content in cows observed in the present study are in line with the higher concentrations of total plasma lipoproteins observed in cattle compared to goats (Vitic and Stevanovic, 1993). Moreover, these data are consistent with those of the recent study carried out on cows and goats using the same methodology (Delavaud et al., 2019). However, the higher concentration in TAG observed in the plasma of goats compared to cows is poorly reported or in very early study (Leat and Baker, 1970). This difference could be due to a higher availability of substrate in the goat intestine for the

Table 5
Plasma fatty acid profile (% of total FA) of triacylglycerols in cows and goats fed either control diet (CTL, $n = 4$) or lipid-supplemented diets with corn oil and starch (COS, $n = 4$), marine algae powder of *Schizochytrium sp.* (MAP, $n = 4$) or hydrogenated palm oil (HPO, $n = 4$).

	Cows				Goats				SEM	Statistical effects, *P*-values [4]		
% of total FA	CTL	COS	MAP	HPO	CTL	COS	MAP	HPO		Species	Diet	Species × Diet
iso14	0.18^{a}	0.05^{bc}	0.04^{c}	0.21^{a}	0.18^{a}	0.15^{a}	0.14^{ab}	0.16^{a}	0.02	0.018	<0.001	0.002
anteiso14	0.37	0.13	0.27	0.34	0.14	0.13	0.21	0.12	0.09	0.047	0.48	0.47
C14:0	1.46^{A}	1.11^{B}	1.64^{A}	1.55^{A}	1.15^{A}	0.83^{B}	1.32^{A}	1.37^{A}	0.09	<0.001	<0.001	0.88
Iso15	0.89^{A}	0.53^{C}	0.60^{B}	0.81^{A}	0.70^{A}	0.36^{C}	0.56^{B}	0.70^{A}	0.04	<0.001	<0.001	0.34
cis-9 C14:1	1.56^{A}	0.98^{C}	1.34^{AB}	1.20^{B}	1.30^{A}	0.89^{C}	1.18^{AB}	1.20^{B}	0.07	0.019	<0.001	0.33
Iso16	1.12^{a}	0.48^{c}	1.01^{ab}	0.87^{a}	0.97^{ab}	0.78^{bc}	1.12^{a}	0.91^{ab}	0.06	0.11	<0.001	0.019
cis-10 C15:1	0.02	0.03	0.09	0.04	0.03	0.03	0.03	0.05	0.02	0.42	0.35	0.44
C16:0	17.5^{B}	16.3^{B}	17.2^{B}	26.3^{A}	19.1^{B}	17.3^{B}	18.2^{B}	25.1^{A}	0.79	0.31	<0.001	0.35
iso17 + *trans*-9 C16:1[1]	1.27^{AB}	1.09^{B}	1.28^{A}	0.88^{B}	1.50^{AB}	1.37^{B}	2.00^{A}	1.38^{B}	0.12	<0.001	0.001	0.14
trans-11 C16:1	0.67	0.56	0.52	0.56	0.74	0.67	0.75	0.74	0.08	0.007	0.60	0.61
cis-9 C16:1 + anteiso17[2]	1.58^{a}	1.25^{ab}	0.99^{b}	1.29^{ab}	1.54^{a}	1.12^{b}	1.27^{ab}	1.47^{a}	0.09	0.17^{5}	$<0.001^{5}$	0.021^{5}
cis-11 C16:1	2.81^{B}	0.61^{C}	5.38^{A}	1.76^{B}	3.38^{B}	0.93^{C}	7.38^{A}	2.91^{B}	0.47	0.005	<0.001	0.27
C17:0	1.28^{A}	0.84^{C}	1.01^{B}	1.00^{B}	1.40^{A}	0.84^{C}	1.08^{B}	1.20^{B}	0.06	0.038	<0.001	0.43
iso18	0.07^{A}	0.01^{B}	0.01^{B}	0.04^{AB}	0.17^{A}	0.06^{B}	0.06^{B}	0.08^{AB}	0.03	0.002	0.015	0.78
cis-9 C17:1	0.06	0.15	0.01	0.06	0.19	0.13	0.09	0.18	0.04	$<0.001^{5}$	0.13^{5}	0.72^{5}
cis-10 C17:1	0.11	0.14	0.43	0.35	0.19	0.13	0.27	0.24	0.11	0.51	0.15	0.72
C18:0	35.5^{a}	25.5^{b}	13.4^{c}	35.0^{a}	32.7^{ab}	38.8^{a}	8.73^{c}	31.1^{ab}	1.76	0.68	<0.001	<0.001
trans-5 C18:1	0.01^{c}	0.21^{a}	0.01^{c}	0.01^{c}	0.01^{c}	0.03^{bc}	0.18^{ab}	0.02^{bc}	0.04	0.82	0.009	0.001
trans-9 C18:1	0.42^{cd}	0.74^{ab}	1.83^{ab}	0.37^{d}	1.10^{abc}	1.31^{ab}	2.64^{a}	0.71^{bcd}	0.37	0.017^{5}	$<0.001^{5}$	0.037^{5}
trans-10 C18:1	0.88^{de}	10.1^{a}	4.37^{b}	0.70^{e}	1.92^{bcd}	2.45^{bc}	4.44^{b}	1.23^{cde}	0.63	0.85^{5}	$<0.001^{5}$	$<0.001^{5}$
trans-11 C18:1	2.68^{B}	2.68^{B}	6.91^{A}	1.90^{B}	2.77^{B}	4.50^{B}	8.32^{A}	3.02^{B}	0.71	0.040	<0.001	0.66
trans-10 / *trans*-11 C18:1	0.33^{b}	3.82^{a}	0.66^{b}	0.36^{b}	0.81^{b}	0.75^{b}	0.64^{b}	0.41^{b}	0.21	<0.001	<0.001	<0.001
trans-12 C18:1	0.52^{C}	1.26^{B}	1.68^{A}	0.38^{C}	0.61^{C}	0.86^{B}	1.60^{A}	0.47^{C}	0.13	0.42	<0.001	0.23
trans-13 C18:1	1.74^{C}	2.61^{AB}	3.22^{A}	1.36^{BC}	0.87^{C}	2.29^{AB}	2.97^{A}	2.31^{BC}	0.37	0.63	<0.001	0.085
cis-9 C18:1	5.13^{cd}	6.58^{bc}	2.93^{d}	4.22^{cd}	10.3^{a}	8.74^{ab}	4.29^{cd}	8.00^{ab}	0.55	<0.001	<0.001	0.009
cis-10 C18:1	0.48^{B}	0.67^{B}	1.29^{A}	0.38^{B}	0.36^{B}	0.53^{B}	1.05^{A}	0.33^{B}	0.10	0.089	<0.001	0.84
cis-11 C18:1	0.57^{abc}	0.77^{ab}	0.62^{abc}	0.49^{c}	0.59^{abc}	0.51^{bc}	0.79^{a}	0.49^{c}	0.06	0.62	0.008	0.010
cis-12 C18:1	0.31^{bcd}	0.60^{a}	0.17^{d}	0.26^{cd}	0.36^{bc}	0.45^{ab}	0.20^{cd}	0.34^{bcd}	0.04	0.89	<0.001	0.020
cis-13 C18:1	0.09	0.17	0.26	0.11	0.10	0.16	0.11	0.08	0.06	0.28	0.30	0.53
cis-14 C18:1 + *trans*-16 C18:1 [3]	0.67^{B}	0.68^{B}	1.36^{A}	0.39^{C}	0.47^{B}	0.57^{B}	0.81^{A}	0.42^{C}	0.08	0.003^{5}	$<0.001^{5}$	0.078^{5}
cis-15 C18:1 + C19:0 [3]	0.07	0.05	0.21	0.06	0.10	0.16	0.17	0.09	0.05	0.30	0.082	0.49
cis-9, *cis*-12 C18:2	7.33	9.29	5.50	6.29	4.55	5.34	3.99	4.36	1.08	$<0.001^{5}$	0.16^{5}	0.93^{5}
C20:0	0.54^{A}	0.42^{B}	0.55^{AB}	0.49^{AB}	0.44^{A}	0.39^{B}	0.39^{AB}	0.40^{AB}	0.03	<0.001	0.038	0.15
C18:3n-6	0.32^{a}	0.27^{a}	0.05^{b}	0.23^{a}	0.17^{ab}	0.18^{ab}	0.18^{ab}	0.16^{ab}	0.03	0.079	0.005	0.004
cis-11 C20:1 + C18:3n-3 [3]	2.27	1.72	1.86	2.05	1.27	1.01	1.36	1.27	0.21	<0.001	0.16	0.57
cis-9, *trans*-11 CLA	0.18^{a}	0.37^{a}	0.35^{ab}	0.08^{b}	0.25^{a}	0.24^{a}	0.37^{a}	0.17^{a}	0.06	0.019^{5}	0.017^{5}	0.039^{5}
C21:0	0.24^{A}	0.07^{B}	0.21^{A}	0.12^{AB}	0.12^{A}	0.07^{B}	0.12^{A}	0.15^{AB}	0.03	0.066	0.013	0.11
trans-9, *trans*-11 CLA	0.37^{b}	0.61^{a}	0.34^{b}	0.24^{b}	0.24^{b}	0.22^{b}	0.25^{b}	0.24^{b}	0.04	<0.001	<0.001	<0.001
C20:2n-6	0.06^{B}	0.07^{AB}	0.21^{A}	0.10^{B}	0.03^{B}	0.02^{AB}	0.05^{A}	0.07^{AB}	0.03	0.007	0.033	0.16
C22:0	0.40^{AB}	0.26^{C}	0.47^{A}	0.29^{BC}	0.28^{AB}	0.14^{C}	0.26^{A}	0.18^{BC}	0.04	<0.001	<0.001	0.56
C20:3n-6	0.34	0.31	0.30	0.25	0.12	0.06	0.17	0.09	0.04	<0.001	0.33	0.46
cis-13 C22:1	0.01^{AB}	0.01^{B}	0.07^{A}	0.01^{B}	0.03^{AB}	0.01^{B}	0.11^{A}	0.01^{B}	0.03	0.013^{5}	0.004^{5}	0.079^{5}
C20:3n-3	0.01^{AB}	0.01^{B}	0.17^{A}	0.01^{B}	0.03^{AB}	0.02^{B}	0.08^{A}	0.03^{B}	0.03	0.064^{5}	0.008^{5}	0.32^{5}
C20:4n-6	0.37^{B}	0.58^{B}	1.17^{A}	0.34^{B}	0.69^{B}	0.58^{B}	1.49^{A}	0.62^{B}	0.09	0.001	<0.001	0.20
C23:0	0.54^{A}	0.24^{B}	0.54^{AB}	0.47^{AB}	0.44^{A}	0.17^{B}	0.31^{AB}	0.35^{AB}	0.10	0.083	0.052	0.87
C22:2n-6	0.15	0.08	0.24	0.21	0.07	0.02	0.10	0.08	0.05	0.005	0.072	0.76
C20:5n-3	0.41^{B}	0.74^{B}	2.74^{A}	0.40^{B}	0.37^{B}	0.31^{B}	2.41^{A}	0.36^{B}	0.23	0.18^{5}	$<0.001^{5}$	0.33^{5}
C24:0	0.44^{B}	0.29^{C}	0.83^{A}	0.41^{B}	0.34^{B}	0.16^{C}	0.52^{A}	0.26^{B}	0.05	$<0.001^{5}$	$<0.001^{5}$	0.41^{5}
C24:1n-9	0.19	0.01	0.10	0.12	0.14	0.05	0.11	0.11	0.06	1.00	0.12	0.84
C22:5n-3	0.42^{B}	0.52^{B}	1.43^{A}	0.29^{B}	0.50^{B}	0.37^{B}	1.49^{A}	0.44^{B}	0.08	0.54	<0.001	0.30
C22:6n-3	0.39^{c}	1.04^{c}	6.84^{b}	0.28^{c}	0.59^{c}	0.76^{c}	9.26^{a}	0.59^{c}	0.34	0.009	<0.001	0.002

Abbreviation: CLA = conjugated linoleic acid.
1 to 5, see footnotes of Table 4.

synthesis of TAG-rich lipoproteins such as chylomicrons or very-low-density lipoproteins, or to a slower turnover of these TAG-rich lipoproteins in goat than in cow plasma. In agreement with the former, a previous study comparing ruminal lipid metabolism in dairy cows and goats fed diets supplemented with starch, plant oil or fish oil showed that rumen fluid has a higher total FA concentration in goats than cows, suggesting a higher bioavailability of FA for intestine TAG synthesis (Toral et al., 2016). This finding agrees with the specificities of cows and goats in their feeding behaviour and digestive processes that were shown by Martin et al. (2021): even though eating and rumination duration were similar in both species, goats had more eating bouts per day, spent less time eating and ruminating comparing to cows. These specificities may contribute to differences among species in FA reaching the intestine for TAG-rich particle secretion. Taken together, these results suggest an incorporation of lipids into lipoproteins transported in plasma specific to ruminant species. The plasma concentration of TAG results from fat secreted by the intestine in the form of chylomicrons and very-low-density lipoproteins and, to a lesser extent, from endogenous sources via hepatic synthesis of very-low-density lipoproteins.

In the present study, the composition of the plasma TAG observed in goats showed a higher content in *cis*-9 C18:1, which was consistent with higher unsaturated molecular species of TAG observed in goats by contrast with higher saturated molecular species of TAG observed in cows. Regarding ceramides composition, the higher plasma ceramide d18:1–16:0 in cows than in goats could be attributed to a between-species difference in the activity

Table 6
Plasma triacylglycerol (TAG) molecular species (% of total TAG) in cows and goats fed either a control diet (CTL, $n = 4$) or lipid-supplemented diets with corn oil and starch (COS, $n = 4$), marine algae powder of *Schizochytrium sp.* (MAP, $n = 4$) or hydrogenated palm oil (HPO, $n = 4$).

	Cows				Goats				SEM	Statistical effects, *P*-values[1]		
% of total TAG	CTL	COS	MAP	HPO	CTL	COS	MAP	HPO		Species	Diet	Species × Diet
24:0	0.47^{a}	0.25^{abc}	0.37^{ab}	0.35^{abc}	0.13^{c}	0.25^{abc}	0.22^{bc}	0.20^{bc}	0.05	<0.001	0.76	0.025
36:0	6.15^{a}	3.24^{abc}	4.94^{abc}	5.27^{ab}	1.98^{c}	3.23^{abc}	2.38^{bc}	2.64^{bc}	0.68	<0.001	0.67	0.063
38:0	6.68^{a}	3.48^{abc}	4.99^{abc}	5.84^{ab}	2.00^{c}	3.56^{abc}	2.31^{bc}	2.39^{bc}	0.74	<0.001	0.68	0.040
38:1	0.17	0.12	0.16	0.16	0.06	0.05	0.05	0.06	0.02	<0.001	0.51	0.67
40:0	3.97	2.47	3.19	4.58	1.39	2.57	2.04	2.37	0.71	0.003[2]	0.68[2]	0.13[2]
40:1	0.13	0.09	0.13	0.12	0.06	0.04	0.05	0.04	0.02	<0.001	0.17	0.88
42:0	2.97	1.79	2.57	2.83	1.09	1.76	1.39	1.48	0.38	<0.001	0.82	0.17
44:0	2.52^{abc}	1.64^{bcd}	3.18^{a}	2.58^{ab}	0.90^{d}	1.21^{cd}	1.41^{bcd}	1.24^{d}	0.26	<0.001	0.027	0.099
44:1	0.21^{B}	0.29^{AB}	0.28^{A}	0.25^{AB}	0.16^{B}	0.15^{AB}	0.28^{A}	0.17^{AB}	0.03	0.005	0.028	0.15
46:0	3.94^{a}	2.23^{bc}	3.23^{ab}	4.06^{a}	2.11^{bc}	2.26^{bc}	1.96^{c}	2.20^{bc}	0.26	<0.001	0.013	0.008
46:1	1.15^{a}	1.07^{a}	1.18^{a}	1.12^{a}	0.73^{c}	0.64^{c}	1.03^{ab}	0.76^{bc}	0.07	<0.001	0.005	0.095
46:2	0.23^{abc}	0.32^{a}	0.29^{ab}	0.24^{abc}	0.18^{bc}	0.16^{c}	0.34^{a}	0.18^{c}	0.04	0.002[2]	0.003[2]	0.029[2]
48:0	4.98^{ab}	2.56^{c}	3.45^{bc}	5.35^{a}	3.00^{c}	3.31^{bc}	2.0^{c}	2.95^{c}	0.37	<0.001	0.002	0.003
48:1	5.98^{A}	4.84^{B}	5.22^{AB}	5.81^{AB}	5.03^{A}	4.05^{B}	4.90^{AB}	4.74^{AB}	0.26	0.004	0.040	0.67
48:2	1.32	1.29	1.23	1.21	1.40	1.09	1.63	1.39	0.11	0.19	0.25	0.12
48:3	0.11^{bc}	0.18^{bc}	0.03^{c}	0.01^{c}	0.27^{ab}	0.16^{bc}	0.42^{a}	0.28^{ab}	0.05	<0.001	0.44	0.006
50:1	1.94^{ab}	0.86^{c}	0.69^{c}	2.36^{a}	1.03^{c}	1.22^{bc}	0.55^{c}	1.08^{c}	0.14[3]	<0.001	<0.001	<0.001
50:2	7.22^{AB}	7.38^{AB}	5.25^{B}	10.0^{A}	7.60^{AB}	7.42^{AB}	5.71^{B}	7.67^{A}	1.08[4]	0.65	0.043	0.54
50:3	3.53^{d}	4.02^{cd}	4.09^{cd}	3.56^{d}	4.94^{ab}	4.03^{bcd}	5.53^{a}	4.85^{abc}	0.19	<0.001	0.006	0.004
50:4	1.05^{c}	1.31^{bc}	1.05^{c}	1.01^{c}	2.27^{a}	1.54^{abc}	2.16^{a}	2.05^{ab}	0.18	<0.001	0.63	0.060
51:0	2.62^{a}	0.81^{b}	1.01^{b}	2.33^{a}	1.20^{b}	0.86^{b}	1.00^{b}	1.31^{b}	0.11	<0.001	<0.001	<0.001
52:1	8.29^{A}	8.50^{A}	3.97^{B}	11.0^{A}	7.36^{A}	8.70^{A}	2.82^{B}	6.81^{A}	1.19	0.092	<0.001	0.33
52:2	7.87^{c}	14.9^{a}	12.7^{a}	8.49^{bc}	11.5^{abc}	12.3^{ab}	13.5^{a}	11.3^{abc}	0.80	0.061	<0.001	0.007
52:3	3.32^{c}	4.90^{b}	4.42^{bc}	3.11^{c}	8.27^{a}	7.90^{a}	8.69^{a}	7.77^{a}	0.32	<0.001	0.010	0.052
52:4	1.75	2.05	2.16	1.19	4.19	3.12	3.98	3.86	0.36	<0.001	0.38	0.18
52:5	0.24^{AB}	0.21^{B}	0.50^{A}	0.10^{AB}	0.89^{AB}	0.51^{B}	1.09^{A}	0.96^{A}	0.14	<0.001	0.048	0.33
54:0	2.31^{ab}	0.33^{e}	1.32^{cd}	2.54^{a}	1.54^{bcd}	0.69^{de}	1.02^{cde}	1.70^{abc}	0.19	0.008	<0.001	0.021
54:1	4.22	2.90	3.21	2.95	3.42	3.48	3.69	3.64	0.35	0.36	0.33	0.15
54:2	5.27^{bcd}	11.2^{a}	3.69^{bcd}	2.73^{d}	6.10^{bc}	7.27^{b}	3.35^{cd}	5.02^{bcd}	0.70	0.57	<0.001	0.004
54:3	3.74^{bc}	7.46^{a}	7.25^{a}	2.94^{c}	5.17^{abc}	6.26^{ab}	7.28^{a}	4.71^{bc}	0.51	0.18	<0.001	0.042
54:4	2.48	2.76	3.28	1.72	4.66	4.26	4.93	4.53	0.36	<0.001	0.081	0.29
54:5	0.90	0.83	1.90	0.63	2.48	1.57	2.95	2.49	0.32	<0.001[2]	0.005[2]	0.11[2*]
54:6	NQ^{B}	0.13^{B}	2.18^{A}	0.09^{B}	1.43^{B}	0.53^{B}	3.27^{A}	1.70^{B}	0.44	0.002	<0.001	0.58
56:1	0.99^{a}	0.26^{d}	0.81^{ab}	0.54^{bcd}	0.79^{abc}	0.40^{cd}	0.62^{bcd}	0.80^{abc}	0.08	0.99	<0.001	0.015
56:2	0.55	0.36	1.73	0.35	0.80	0.56	1.61	0.94	0.18	0.098	<0.001	0.30
56:3	0.31^{bc}	0.27^{bc}	1.03^{a}	0.15^{c}	0.63^{abc}	0.28^{bc}	0.74^{ab}	0.68^{ab}	0.11	0.072	<0.001	0.005
56:4	0.16^{B}	0.17^{C}	0.82^{A}	0.14^{B}	0.40^{B}	0.15^{C}	1.09^{A}	0.66^{B}	0.12	0.002[2]	<0.001[2]	0.052[2]
58:1	1.37^{A}	1.09^{AB}	0.69^{B}	1.46^{A}	1.32^{A}	1.21^{A}	0.66^{B}	1.15^{A}	0.17	0.60	0.003	0.67
58:2	0.04^{c}	0.12^{bc}	0.32^{a}	0.05^{bc}	0.08^{bc}	0.03^{c}	0.17^{b}	0.09^{bc}	0.03	0.044	<0.001	0.002
58:3	NQ^{b}	NQ^{b}	0.47^{a}	NQ^{b}	NQ^{b}	NQ^{b}	0.13^{b}	NQ^{b}	0.02	0.006	<0.001	<0.001
60:0	0.40^{A}	NQ^{C}	0.25^{B}	0.36^{AB}	0.30^{A}	0.04^{C}	0.16^{B}	0.24^{AB}	0.05	0.062	<0.001	0.41
60:2	0.57^{bc}	1.11^{a}	0.45^{bc}	0.27^{c}	0.81^{ab}	0.77^{ab}	0.48^{bc}	0.63^{bc}	0.08	0.21	<0.001	0.002
60:4	0.19^{bc}	0.23^{abc}	0.38^{ab}	0.10^{c}	0.38^{a}	0.23^{abc}	0.31^{ab}	0.29^{abc}	0.04	0.013	0.006	0.007

Abbreviation: NQ = Not quantifiable, below about E^{-16}.
[1] $^{a-d}$ Least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to species × diet interactions. $^{A-C}$ least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to diet.
[2] *P*-values from statistical analyses performed on log-10 values, * When normalization was not possible, no statistical effect was considered.
[3] SEM was 0.166 for cow CTL and for goat COS because n = 3.
[4] SEM was 1.27 for cow CTL and for goat COS because n = 3.

of ceramide synthase utilizing palmitoyl-CoA for *de novo* ceramide synthesis by liver (Levy and Futerman, 2010) or to a between-species difference in the preferred pathways used for ceramide synthesis (McFadden and Rico, 2019).

Effect of lipid-supplemented diets on plasma lipids in cows and goats

The starch-rich diet supplemented in corn oil increased plasma cholesterol and total lipids in goats, in accordance with previous observation in cows and goats fed diet supplemented with sunflower oil plus starch (5.3% DMI; Delavaud et al. (2019)). Diets supplemented with vegetable lipids were shown to increase plasma lipids, as observed for total lipids, phospholipids and cholesterol esters in lactating cows supplemented with linoleic sunflower oil or grains (8% of DMI) (Steele et al., 1971) and for plasma total lipids in mid-lactation goats supplemented with hemp seed oil (4.7% DMI) (Cozma et al., 2015). However, the absence of increase in total lipids in cows with the COS diet observed in the present study, due to the absence of increase in the cholesterol fraction, suggests species-specificity in cholesterol metabolism. Otherwise, the TAG and FFA concentrations did not change with corn oil and starch supplement for both species, with the FA profiles of the free and TAG fractions being altered mainly in cows. The most notable changes are in the *trans*-10 C18:1, which increased 11.5-fold, in the FA profile of TAG, leading to an 11.6-fold increase in the *trans*-10/*trans*-11 18:1 ratio in the TAG fraction (Table 5) that is specific to COS treatment in cows. These results are in line with the 13.6- and 10.1-fold increases respectively in *trans*-10 C18:1 and *trans*-10/*trans*-11 18:1 ratio in milk of cows fed the COS diet (Fougère et al., 2018). Indeed, due to high starch content in the diet, the classical ruminal biohydrogenation pathway of linoleic acid leading to the synthesis of *trans*-11 isomers such as *cis*-9, *trans*-11 conjugated

Table 7
Plasma ceramide concentration (ng of Ceramide internal standard equivalent/ml plasma) in cows and goats fed control diet (CTL, $n = 4$) or lipid-supplemented diets with corn oil and starch (COS, $n = 4$), marine algae powder of *Schizochytrium sp.* (MAP, $n = 4$) or hydrogenated palm oil (HPO, $n = 4$).

	Cows				Goats				SEM	Statistical effects, *P*-values[1]		
Items	CTL	COS	MAP	HPO	CTL	COS	MAP	HPO		Species	Diet	Species × Diet
d18:1–16:0	158^{ab}	138^{ab}	159^{ab}	192^{a}	65.3^{c}	116^{bc}	75.6^{c}	72.4^{c}	6.26	<0.001	0.37	0.009
d18:1–16:1	4.10^{B}	4.69^{AB}	5.65^{A}	3.76^{B}	1.70^{B}	2.72^{AB}	2.94^{A}	1.74^{B}	0.24	<0.001	0.0015	0.68
d18:1–18:0	15.7^{b}	15.1^{b}	13.6^{b}	18.8^{b}	14.0^{b}	40.3^{a}	10.9^{b}	16.7^{b}	1.01	0.003	<0.001	<0.001
d18:1–18:1	4.80^{B}	5.89^{A}	5.28^{B}	4.35^{B}	2.46^{B}	4.84^{A}	3.48^{B}	2.80^{B}	0.17	<0.001	<0.001	0.31
d18:1–20:0	3.68^{c}	4.82^{bc}	4.08^{bc}	4.08^{bc}	6.49^{bc}	12.7^{a}	7.50^{b}	6.86^{bc}	0.38	<0.001	<0.001	0.007
d18:1–22:0	35.2^{d}	55.7^{cd}	90.2^{bc}	50.4^{cd}	70.1^{bcd}	167^{a}	119^{ab}	78.1^{bcd}	5.97	0.001	<0.001	0.002
d18:1–24:0	130^{c}	192^{bc}	296^{ab}	179^{bc}	18^{bc}	432^{a}	350^{a}	205^{bc}	15.7	0.006	<0.001	0.005
d18:1–24:1	33.1^{c}	47.2^{c}	89.6^{a}	44.8^{c}	48.7^{c}	82.0^{ab}	82.6^{a}	53.5^{bc}	3.25	0.030	<0.001	0.020
d18:1–26:0	6.10^{c}	8.41^{c}	10.4^{c}	7.89^{c}	8.78^{c}	23.6^{a}	21.4^{ab}	11.3^{bc}	1.13	<0.001[2]	<0.001[2]	0.067[2]
d18:1–26:1	2.10^{B}	2.40^{AB}	3.37^{A}	2.20^{B}	2.57^{B}	3.88^{AB}	4.07^{A}	2.78^{B}	0.15	0.001	<0.001	0.36
Sum of Cer	393^{c}	474^{bc}	678^{ab}	507^{bc}	403^{bc}	885^{a}	678^{abc}	452^{bc}	58.3	0.084	<0.001	0.003

[1] $^{a-d}$ Least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to species × diet interactions. $^{A-C}$ least square means within a row that do not share a common superscript letter differ ($P < 0.05$) due to diet.
[2] *P*-values from statistical analyses performed on log-10 values.

linoleic acid and *trans*-11 C18:1 switches to the *trans*-10 pathway, which results in the synthesis of *trans*-10 C18:1 and C18:2 isomers, associated with MFD in cows (Shingfield et al., 2010). However, in the present experimental conditions, the *trans*-10, *cis*-12-18:2 isomer was not detected in the plasma TG or FFA for cows, despite its presence in milk (Fougère et al., 2018). That was previously observed in cows (Delavaud et al., 2019, Loor et al., 2002), and probably, other plasma fractions like PL or cholesterol esters could carry this conjugated linoleic acid isomer. In goats, for which no MFD was observed with COS, neither *trans*-10 nor *trans*-11 isomers increased in plasma TAG or free FA profiles, which is in line with the absence of variation in milk *trans*-10 C18:1 content (Fougère et al., 2018). This observation, combined with a higher proportion of C18:0 in TAG of goats compared to cows, suggests a more complete ruminal biohydrogenation of linoleic acid which could be related to observed differences in feeding behaviour (Martin et al., 2021) and rumen bacterial community (Toral et al., 2016) among these species. Furthermore, in cows, the specific decrease in C16:0 in the plasma free FA profile and in the sum of < C16:0 FA in the TAG and free FA profiles could also contribute to COS-induced MFD by reducing the availability of short- and medium-chain FA for mammary TAG synthesis. This occurs in addition to the specific decrease in cows of the sum of C18:0 and C18:1 *cis*-9 in the TAG (-21%) and free FA (-18%) fractions with COS compared to CTL. Thus, a shortage of FA available for the mammary gland could contribute to the MFD observed with COS diet in cows. This is in line with a study of the same experiment which reported little or no variation in mammary mRNA and enzyme activities in cows with this treatment (Fougère and Bernard, 2019). Looking at the composition in molecular species of TAG, the correlations between them and the TAG FA profiles provided further clues to the possible role of specific biologicallyactive FA on plasma TAG composition. Indeed, TAGs 54:3 and 52:2, which were specifically increased in cows fed COS, were highly correlated to plasma *trans* FA, particularly *trans*-10 C18:1 ($r = 0.846$ and $r = 0.831$, $P < 0.0001$, respectively) which is one of the most salient indicators of MFD (Shingfield et al., 2010). In other respects, the COS diet increased the sum of plasma ceramides in goats but not in cows. Only a few papers have studied the link between ceramides and milk production parameters, the most relevant showing a positive relationship between plasma 22:0-, 24:0- and 26:0-ceramides and milk yield in mid-lactation cows (Rico et al., 2016). In the present study, an increase of these ceramide molecular species was observed in goats fed COS, which was associated with an absence of decrease in milk fat unlike the cows for which milk fat concentration decreased and ceramides did not vary. These data in goats could suggest that higher ceramide concentration would increase insulin resistance promoting long-chain FA release by adipose tissue in favour of milk fat synthesis, which would contribute to explain species-specificities in the response to MFD diets. However, under our experimental conditions, no clear link could be established between plasma ceramides data and milk fat synthesis, whereas the mammary uptake of plasma FA with antilipogenic effects is a possible explicative mechanism of diet-induced MFD.

The addition of MAP, that depressed milk fat concentration in cows and goats in the present study, increased cholesterol, cholesterol esters and PL in plasma, whereas FFA and TAG concentrations remained unaffected. These observations together with the low apparent transfer rate of docosahexaenoic acid into the milk (12% for cows and 7% for goats; Fougère et al. (2018)) suggest that the docosahexaenoic acid escaping from ruminal biohydrogenation and its biohydrogenation products would be substantially esterified in cholesterol esters and PL, unavailable for mammary uptake. These results are in accordance with data on mid-lactation cows fed a fish oil-supplemented diet showing a low rate of transfer of long-chain *n-3* FA which was attributed to extensive docosahexaenoic acid integration in cholesterol esters and PL of plasma HDL and, to a lesser extent, in TAG and PL of low-density lipoproteins (Offer et al., 2001). In addition, and as observed in milk FA composition (Fougère et al., 2018), the sum of *trans* C18:1, docosahexaenoic acid and eicosapentaenoic acid increased in both free FA and FA of TAG profiles. Moreover, the specific increase in the proportion of plasma docosapentaenoic acid in free FA in cows was also observed in milk as the increase of plasma *trans*-11 C18:1 in free and TAG FA profiles for both species with those of *trans*-11 C18:1 and *cis*-9, *trans*-11 conjugated linoleic acid in the milk of cows and goats fed MAP (Fougère et al., 2018). This suggests a synthesis of *cis*-9, *trans*-11 conjugated linoleic acid from the *trans*-11 C18:1 by the mammary gland stearoyl-CoA-desaturase as previously reported (AbuGhazaleh et al., 2003; Bernard et al., 2010). The main species-specific response of plasma FA to MAP was an increase in *trans*-10 and *trans*-11 C18:1 in the TAG FA profile of cows, as observed in milk, probably due to the mammary gland uptake of these FAs. Although MAP induced MFD in both cows and goats, our results showed different patterns of response in free and TAG FA profiles between the two species, which points to species-related specificities in rumen and post-absorptive lipid metabolism whereas no difference in mammary metabolism was

observed (Fougère and Bernard, 2019). As previously observed for the COS diet, MAP specifically increased TAGs 54:3 and 52:2 and *trans*-10 C18:1 in plasma free and TAG FA profiles of cows, whereas TAGs 46:1 and 46:2 were specifically increased by MAP in goats and positively correlated to the main plasma FAs increased by MAP, such as docosahexaenoic acid ($r = 0.754$ and $r = 0.764$, $P = 0.001$, respectively), docosapentaenoic acid ($r = 0.740$, $P = 0.002$, and $r = 0.780$, $P = 0.001$, respectively), and eicosapentaenoic acid ($r = 0.586$, $P = 0.022$, and $r = 0.636$, $P = 0.011$, respectively). These data suggest that docosahexaenoic acid, docosapentaenoic acid and eicosapentaenoic acid could be involved in the changes in plasma abundances of these molecular species of TAGs. Furthermore, in both cows and goats, TAG 56:4 was strongly correlated to the sum of plasma *n-3* FA ($r = 0.908$, $P < 0.0001$, $n = 32$), which are particularly present in the MAP diet. The specific increase in plasma TAGs 54:3 and 52:2 in cows (with COS and MAP) and TAGs 46:1 and 46:2 in goats (with MAP) could be considered as plasma markers of MFD in these animal species and thus warrants further investigation. Our results suggest that the large variations in lipid plasma molecules in cows and goats fed the MAP diet could be related to the MFD observed in both species.

The HPO added to the diets of cows and goats, shown to increase milk fat concentration of cows, had no impact on plasma lipid concentrations whatever species. However, while the C16:0 proportion of the TAG FA profile increased in both species, an enrichment of 16-carbon FA resulting from an increase of C16:0 was observed only in milk of cows fed HPO (Fougère et al., 2018). Taken together, these results suggest that the between-species differences in milk fat concentration and C16:0 proportion, in response to HPO, result from differences in the availability and mammary gland uptake of C16-chain FA.

Conclusion

The direct comparison of plasma lipid classes and compositions in cows and goats in response to diets supplemented or not with various lipids argues in favour of a species-specific regulation. These specificities between species contribute to explain the differences in milk fat content observed with the diets, with essentially a greater availability of the plasma TAG fraction for mammary gland uptake in goats and a higher content of FA with antilipogenic effects in free and TAG FA profiles in cows. Indeed, plasma total lipid content was higher in cows than in goats, whereas plasma TAG concentration was lower in cows than in goats. The COS diet increased plasma total lipids, cholesterol and the sum of ceramides only in goats. Regarding the free and TAG FA profiles, the *trans*-10 C18:1 was only increased in cows, in favour of its higher availability for mammary gland uptake and biological role in MFD. In cows and goats, the MAP diet increased plasma total lipids, cholesterol esters, cholesterol, PL, saturated very long-chain ceramides and the sum of *trans* C18:1, eicosapentaenoic acid and docosahexaenoic acid in free and TAG FA profiles, which were thus available for mammary gland uptake. The HPO diet had no effect on plasma total lipids and lipid classes, but increased the proportion in C16:0 of TAG FA profile in cows and goats. Our results suggest firstly that, in our experimental conditions, mammary uptake of plasma FA with antilipogenic effects is the main explicative mechanism of diet-induced MFD and secondly that there is more TAG available for mammary uptake in goats, which makes the goat less prone to diet-induced MFD. The implication of ceramides in the specific response of the goats would need further investigation. These data provide valuable clues to help decipher the underlying mechanisms controlling milk fat plasticity and more generally the comparative physiology of lactation. In particular, the hypothesis of a lower turnover rate of circulating TAG particle in goats would require further study.

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2022.100635.

Ethics approval

The Auvergne Rhone-Alpes institutional animal care and use committee issued approval for all the planned experimental procedures (France; DGRI agreement APAFIS#3277-2015121411432527v5), which were compliant with the guidelines established by European Union Directive 2010/63/EU on the protection of animals used for scientific purposes.

Data and model availability statement

The Dataset on plasma polar lipid composition can be viewed in the Recherche Data Gouv repository, at https://doi.org/10.57745/VYTZ5R. The use of data is restricted to scientific and non-commercial use.

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Declaration of interest

None.

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