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Metabolic and hormonal control of energy utilization and partitioning from early to mid lactation in Sarda ewes and Saanen goats

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ABSTRACT

In a recent study, we observed that starch-rich diets used in mid lactation induced lower milk production persistency and higher body fat accumulation in dairy ewes compared with dairy goats. Because these species differences could be linked to hormonal mechanisms that drive energy partitioning, in the same experiment, we explored the evolution of metabolic and hormonal status during lactation to test this hypothesis. Twenty mature Sarda dairy ewes and 20 mature Saanen goats [15–134 ± 11 d in milk (DIM), mean ± SD] were compared simultaneously. In early lactation, each species was allocated to one dietary treatment: high-starch diet [HS: 20.4% starch, on dry matter (DM) basis], whereas from 92 ± 11 DIM, each species was allocated to 1 of 2 dietary treatments: HS (20.0% starch, on DM basis) and low-starch (LS: 7.8% starch, on DM basis) diets. Blood samples were collected in the morning to analyze glucose, nonesterified fatty acids (NEFA), growth hormone (GH), insulin, and insulin-like growth factor I (IGF-I). Data were analyzed using the PROC MIXED procedure of SAS with repeated measurements (SAS Version 9.0). The HS and LS diets applied in mid lactation did not affect metabolic status of the animal within species; thus, only a comparison between species was carried out. From early to mid lactation, plasma glucose concentration was higher in ewes than in goats (54.57 vs. 48.35 ± 1.18 mg/dL), whereas plasma NEFA concentration was greater in goats than in ewes (0.31 vs. 0.25 ± 0.03 mmol/L). Goats had higher plasma GH concentration and lower plasma insulin content than ewes (4.78 vs. 1.31 ng/mL ± 0.47; 0.11 vs. 0.26 μg/L ± 0.02). Plasma IGF-I concentration did not vary between species. The comparison of metabolic and hormonal status of lactating Sarda dairy ewes and Saanen goats, carried out by studying simultaneously the 2 species in the same stage of lactation and experimental conditions, suggests that the higher insulin and glucose concentration observed in Sarda ewes explains why they partitioned more energy toward body reserves than to the mammary gland, especially in mid lactation. This can justify the negative effect of high-starch diets in mid-lactating Sarda ewes. Conversely, the highest GH and NEFA concentration observed in Saanen goats explain why they partitioned more energy of starch diets toward the mammary gland than to body reserves and justify the positive effect of high-starch diet in mid lactation. Together, these different responses contribute to explain why specialized dairy goats, such as the Saanen breed, have a higher milk production persistency than specialized dairy sheep breeds, such as the Sarda.
Key words: energy partitioning, hormonal status, starch, ewe, goat

INTRODUCTION

Ewes and goats are both small ruminants but differ to a certain extent in their feeding behavior and selectivity, milk production, and possibly their nutrient utilization and metabolism. Hofmann (1989) classified goats as intermediate feeders and ewes as grass and roughage eaters, differing in their feeding preferences and selectivity, with goats more prone to browse and be more selective and ewes more devoted to grazing herbaceous swards. Other differences regard their milk production. Indeed, ewes in general are less productive with shorter lactations and produce milk with much higher fat and protein concentrations compared with goats.

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Regarding the utilization of nutrients, various experiments conducted using sheep and goats individually observed a different response during lactation when fed starch or highly digestible fiber diets. In early lactation, when the energy balance is often negative, high-starch diets favor milk production in both species. In mid lactation, the effect of high-starch diets gave contrasting results between the 2 species (Lunesu et al., 2017). Specifically, in mid-lactating dairy ewes, some experiments showed that diets rich in highly digestible fiber (e.g., high content of beet pulps or soybean hulls) increased milk production, whereas high-starch diets stimulated body fat deposition (Bovera et al., 2004; Cannas et al., 2004, 2013). Conversely, a positive effect of highly digestible fiber in mid lactation has not been observed in goats, which responded positively to high-starch diets also in this lactation stage (Cannas et al., 2007; Ibáñez et al., 2015).

These different responses could be due to species differences in the concentration of the hormones, growth hormone (**GH**) and insulin, which controls energy partitioning, or in the responsiveness of tissues involved in the energy partitioning and blood glucose utilization in mid lactation. Differences in the hormonal status of these species in mid lactation can be innate or due to the effect of genetic selection for milk production, likely more intense in goats than ewes. It is well known that the hormonal status during the lactation affects the energy partitioning toward fetus, mammary gland, or body reserves (Bauman and Currie, 1980; Peel and Bauman, 1987; Sasaki, 2002). Indeed, in early lactation, when the requirements of animals are high and the energy balance is negative, the nutrients are usually directed to the mammary gland, whereas later on, when the energy of diet exceeds the requirements of the animals, nutrients are stored as body fat (Bauman and Currie, 1980; Svennersten-Sjaunja and Olsson, 2005). Probably variations in GH and insulin concentration drive nutrient partitioning toward milk production or body reserves. However, the information available in the literature on the evolution of the hormones controlling energy partitioning during the lactation refers mostly to large ruminants, whereas information related to dairy goats and dairy ewes is limited, and no studies have compared the evolution of the hormonal status of lactating goats and ewes fed the same diet under the same environmental conditions.

Thus, the aim of this work was to (1) study the evolution of the metabolic and hormonal status that drives energy utilization and partitioning during the lactation in Saanen goats and Sarda ewes, and (2) understand if the probably different response in the use of carbohydrates (i.e., starch or highly digestible fiber) during lactation can be explained by their hormonal status.

MATERIALS AND METHODS

The experiment was conducted at the Olmedo-Bonassai experimental farm of the Agricultural Research Agency of Sardinia (AGRIS), located in the north west of Sardinia, Italy (40°N, 32°E, 32 m above sea level). The animal protocol described below complied with European Union and Italian regulations on animal welfare, and all measurements were taken by personnel previously trained and authorized by the institutional authorities managing ethical issues at the University of Sassari and AGRIS.

Experimental Procedure: Animals and Diets

Twenty mature Sarda dairy ewes and 20 mature Saanen goats, homogeneous for age (5 yr old) and for lactation number (n = 4), were monitored from January until June 2015 (i.e., 15–134 ± 11 DIM; mean ± SD). The health status of sheep and goats was monitored during the trial by a veterinary staff through the evaluation of the hematological and biochemical parameters, body condition, feces, and milk composition.

The ewes and the goats were kept inside a closed barn, in 4 large pens (2 per species, 68.4 m^2/pen), each one with an access to an external paddock (54 m^2/each). Each pen had a trough with fresh and clean water, which allowed adequate drinking space for all animals. Before parturition, all the animals were dewormed. Due to the persistency of internal parasites, a second deworming treatment was applied at 69 ± 11 DIM, with the single dosage of 15 mL/goat and 10 mL/ewe of albendazole (Valbazen, Pfizer Italia, Rome). The study was divided in 2 periods, early and mid lactation.

Early Lactation

In early lactation (15–91 ± 11 DIM), all animals were fed a high-starch diet (**HS**; Table 1) containing, as-fed, 32.0% of chopped dehydrated alfalfa, 3.0% of mature ryegrass hay, and 65.0% of high-starch concentrate with 30.0% starch and 27.4% NDF (all values expressed on a DM basis). In addition, whole corn grains were supplied during the 2 daily milkings (200 g/d as-fed, in total). In total, the diet had (on DM basis) 35.4% NDF, 35.5% NFC, 20.4% starch, and 16.2% CP; (Table 1). The ewes and goats were kept with their lambs and kids until they were weaned (around 42 DIM), and then they were milked twice per day in a milking parlor.

Mid Lactation

From 92 to 134 ± 11 DIM, the animals of each species were divided in 2 subgroups and allocated to a

Table 1. Ingredient and chemical composition of the high-starch (HS) and low-starch (LS) diets supplied during the experiment

	Early lactation	Mid lactation	
Diet	HS	HS	LS
Ingredient, % as-fed			
Concentrate (high-starch or low-starch)	65.0	67.0	67.0
Dehydrated chopped alfalfa	32.0	29.0	29.0
Mature ryegrass hay	3.0	4.0	4.0
Total	100.0	100.0	100.0
Concentrate ingredient, % as-fed			
Dehydrated alfalfa	30.5	30.0	30.0
Corn meal	26.9	21.1	3.0
Barley meal	13.4	13.4	0.0
Wheat bran	10.1	10.1	5.0
Soybean hulls	—	9.0	43.2
Soybean meal 44	7.9	5.0	7.4
Sugarcane molasses	4.6	4.6	4.6
Sodium bicarbonate	4.3	3.0	3.0
Bentonite	2.0	2.0	2.0
Magnesium oxide	—	1.5	1.5
Minerals and vitamins	0.3	0.3	0.3
Appetizer	0.03	0.03	0.03
Total	100.0	100.0	100.0
Diet chemical composition			
DM, % as-fed	88.6	89.6	89.1
CP, % of DM	16.2	15.5	15.6
Ash, % of DM	10.7	11.0	11.2
Ether extract, % of DM	2.3	1.4	1.4
NDF, % of DM	35.4	36.7	48.8
ADF, % of DM	21.5	25.6	35.5
ADL, % of DM	3.6	4.7	5.1
NFC,[1] % of DM	35.5	35.4	23.0
Starch, % of DM	20.4	20.0	7.8

[1]NFC = 100 – CP – ash – NDF – ether extract.

HS or low-starch (**LS**) diet. Subgroups were balanced within species to have the same average BCS (goats: 2.84 vs. 2.79, and ewes: 3.39 vs. 3.33, in HS vs. LS diet, respectively) and milk production (goats: 3.13 vs. 3.12 kg/d, and ewes: 1.76 vs. 1.78 kg/d; in HS vs. LS diet, respectively). All the animals were fed a diet (Table 1) containing, as-fed, 29.0% of chopped dehydrated alfalfa, 4.0% of mature ryegrass hay, and 67.0% of the experimental concentrate, which differed depending on the group as follows: (1) for the HS group a high-starch concentrate with 28.1% starch and 30.7% NDF, and (2) for the LS group a low-starch concentrate, composed of 10.0% starch and 48.8% NDF (all values expressed on a DM basis). The concentrates differed mainly because most of the cornmeal and all the barley meal of high-starch concentrate was replaced with soybean hulls, a high source of highly digestible fiber, in the low-starch concentrate. In addition, whole corn grains were supplied during the 2 daily milkings (100 g/d as-fed, in total).

The diets were group fed ad libitum and supplied twice a day immediately after each milking (0700 and 1500 h). Orts were quantified daily and the feed offer was adjusted to guarantee at least 110% of the intake measured the day before.

Measurements and Samplings

Orts were collected and weighed every day. Samples of feeds were collected weekly. Milk production was measured once a week, and milk samples were collected and immediately stored at 4°C until analysis could be carried out (within 2 d from the sampling). Milk production measurement started at an average of 48 DIM, because ewes and goats were kept with their lambs and kids until the latter were weaned (around 42 DIM).

Body condition score and BW were assessed every 2 wk. Blood samples were collected at 15, 21, 49, 78 DIM (early lactation) and at 94, 126, and 134 DIM (mid lactation) after the morning milking and just before the morning meal.

Blood was collected from the jugular vein in vacuum tubes with anticoagulants: lithium heparin (Venosafe VF-109SHL Lithium Heparin, Terumo Europe NV, Leuven, Belgium; 9 mL) for the subsequent determination of hormones; EDTAK3 (Venosafe VF-053STK

Terumo Europe NV, Leuven, Belgium; 3 mL) for the determination of hormones and nonesterified fatty acids (**NEFA**); and glucose-NaF/NH (Vacucheck, Nuova Aptaca s.r.l, Italy; 4 mL) for the determination of glucose. Additional blood samples were collected at 35, 64, and 113 DIM only for GH determination. Blood samples were immediately centrifuged at 1,500 × *g* for 10 min at 4°C to separate plasma, which was collected and stored at −20°C until the samples were assayed.

Chemical Analyses

Feedstuffs and Orts. The samples of feeds and orts were ground with a hammer mill by using a 1-mm screen and then analyzed for DM after drying at 105°C for 24 h. Neutral detergent fiber, ADF, and ADL were analyzed using Ankom filter bag equipment (Ankom Technology Corp., Fairport, NY) and following the methods of Van Soest et al. (1991). The NDF solution included thermostable amylase and did not include sodium sulfite; values were expressed ash-free. In addition, CP (Kjeldahl method; AOAC International, 2000; method 988.05), ash (AOAC International, 2000; method 942.05), and ether extract (**EE**; AOAC International, 2005; method 920.39) were analyzed. The NFC were calculated according to Weiss (1999) as follows: NFC (g/kg of DM) = 100 − (NDF + CP + ash + EE). Starch was measured by polarimetry (Polax 2L, Atago, Tokyo, Japan) according to European Community (1999).

Milk. The morning and afternoon milk samples were analyzed separately for fat, protein (N × 6.38) and lactose content using a Milkoscan 6000 instrument (Foss Electric, Hillerød, Denmark). Milk energy output was calculated as Mcal/d of net energy = [251.73 + 89.64 × PQ + 37.85 × (PP/0.95)] × Yn/1,000 for ewes, and as Mcal/d of net energy = [289.72 + 71.93 × PQ + 48.28 × (PP/0.92)] × Yn/1,000 for goats, according to Tedeschi et al. (2010). In particular, Yn is measured milk yield at a particular day of lactation (kg/d), PQ is measured milk fat at a particular day of lactation (%), and PP is measured true milk protein for a particular day of lactation (%).

Blood. Blood samples were analyzed for glucose, NEFA, GH, IGF-I, and insulin. Glucose and NEFA were analyzed by enzymatic colorimetric assays in both species. Glucose content was analyzed by using glucose kit (glucose oxidase-peroxidase method; Shenzhen Mindray Bio-Medical Electronics Co., Shenzhen, China). The NEFA concentration was determined by using NEFA-HR (2) kit (acyl-CoA synthetase-acyl-CoA oxidase method; Wako Chemicals GmbH, Neuss, Germany).

Plasma concentrations of GH and IGF-I were evaluated by RIA technique. The concentration of IGF-I in plasma samples was analyzed by RIA after an acid/ethanol extraction to release IGF from binding proteins. The RIA was performed according to manufacturer's instructions. The IGF-I was determined using an antibody distributed by Novozymes Biopharma (Thebarton, Australia). Recombinant human IGF-I (Novozymes Biopharma) was used as the radioligand and unlabeled ligand. The tracer was prepared with Na ^{125}I by the iodogen method (Salacinski et al., 1981). The minimum detectable dose of IGF-I was 2.7 pg/tube. Intra- and interassay coefficients of variation were 4.4 and 9.1%, respectively.

Circulating ovine GH was measured by a heterologous double antibody RIA, using a purified oGH preparation (LER 1774) both as the standard and tracer. The tracer was prepared following the methods described by Salacinski et al. (1981) and 10,000 cpm of the ^{125}I-oGH solution (specific activity: 7.7 μCi/μg) obtained were added to each assay tube. The antiserum was raised in the rabbit against oGH (LER 1774) and used at the final dilution of 1/7,000. The antiserum showed a cross-reactivity of 0.1% with bovine prolactin and less than 0.01% with other pituitary hormones. Separation of free hormone from hormone–antibody complexes was achieved using an anti-rabbit gammaglobulin serum raised in the goat at the final dilution of 1/500. The sensibility of the analyses, in terms of the interpolated dose as a response to zero concentration, minus the statistical error (Programme Riastar, Canberra-Packard, Schwadorf, Austria), was 0.28 ng/mL. The precision of the method, within assay and between assays, evaluated with repeated doses of a sample of plasma fluid, was expressed by the coefficient of variation, with values of 6.5 and 11.8%, respectively.

Insulin was analyzed through a solid-phase 2-site enzyme immunoassay based on the direct sandwich technique, in which 2 monoclonal antibodies are directed against separate antigenic determinants on the insulin molecules by using insulin ELISA kits (Mercodia AB, Uppsala, Sweden). The sensitivity was equal to 0.025 μg/L, and the intra- and interassay coefficients of variation were 3.6 and 6.4%, respectively.

Statistical Analyses

Data were analyzed by the PROC MIXED procedure of SAS (Version 9.0, SAS Institute Inc., Cary, NC) accounting for repeated measurements. In early lactation, the model included the fixed effect of species (2 species, sheep and goats), the effect of period, their interac-

tions, and the random effect of animal. In mid lactation, a mixed model was used to test the effect of diet within species (HS and LS), the effect of period, species × period interaction, and the random effect of animal.

For milk production, BCS and BW data of the preliminary period (92 ± 11 DIM) were included in the model as covariate. Data were expressed as mean ± standard error of the mean. Means were separated using Tukey's test. The accepted level of significance was $P < 0.05$.

RESULTS

Evolution of Feed Intake, Milk Production and Body Reserves

The evolution of DM intake, milk yield, milk energy output, fat-to-protein ratio, BW, and BCS, are shown in Figures 1, 2, and 3. Group average DM intake was similar between the 2 species during the whole experiment (Figure 1). After the change of the diet (from 92 DIM), on average, the 2 groups of goats had very similar DM intake (Figure 1A), whereas the average group DM intake in the ewes was lower for the HS than for the LS diet (Figure 1B).

From 92 DIM and until the end of experiment (134 DIM), when feeding treatments were applied, milk yield (2.66 vs. 2.53 ± 0.04 kg/d, for HS and LS, respectively; $P < 0.05$. Figure 2A), 3.5% FCM (2.65 vs. 2.53 ± 0.05 kg/d for HS and LS, respectively; $P < 0.05$), and milk energy output (1.88 vs. 1.80 ± 0.03 Mcal/d for HS and LS, respectively; $P < 0.05$; Figure 2B) were significantly higher in the HS than in the LS goats. In addition, the fat-to-protein ratio did not differ between the 2 diets (1.12 vs 1.15 ± 0.02; for HS and LS, respectively; Figure 2C). Conversely, in ewes milk yield from 92 DIM did not differ, but 6.5% FCM yield (1.47 vs. 1.36 ± 0.04 kg/d; for LS and HS, respectively; $P < 0.01$) and milk energy output (1.53 vs. 1.41 ± 0.04 Mcal/d; for LS and HS, respectively; $P < 0.01$; Figure 2B) were significantly higher in the LS than in the HS ewes. The fat-to-protein ratio did not differ between the 2 diets (1.27 vs 1.29 ± 0.01; for HS and LS, respectively; Figure 2C). In goats, BCS was lowest at parturition and increased very slowly until DIM 78 and then remained almost constant until the end of the experiment (Figure 3A). In ewes, BCS was lowest at parturition and markedly increased as lactation progressed (Figure 3A). From 92 DIM, the BCS was higher in the HS than in the LS ewes (3.53 vs. 3.38 ± 0.05; $P < 0.01$). In goats it did not differ between the 2 dietary treatments applied after 92 DIM.

Body weight (Figure 3B) increased in both species throughout the experiment, but it was not affected by the feeding treatments applied in mid lactation (starting at 92 DIM) in goats or sheep.

Evolution of Metabolites and Hormones During Lactation

Plasma glucose concentration was higher in ewes than in goats [54.57 vs. 48.35 mg/dL ± 1.18 (mean values from 15–134 DIM ± SEM); $P < 0.0001$]. Even though the effect of period was significant, the variations in glucose concentration during the lactation were limited (Figure 4A). In both species, the value was highest in early lactation, especially at DIM 21 and 49, then decreased until DIM 94, to increase again, especially in ewes, at the end of the experiment (DIM 126 and 134). Plasma NEFA concentration was higher in goats than in ewes (0.31 vs. 0.25 mmol/L ± 0.03; $P = 0.036$) with much higher values, for both species, in early than mid lactation (effect of period: $P < 0.0001$; Figure 4B). Goats had higher plasma GH (4.78 vs. 1.31 ng/mL ± 0.47; $P < 0.0001$; Figure 5A) and lower insulin concentration (0.11 vs. 0.26 μg/L ± 0.02; $P < 0.0001$; Figure 5B) than ewes. The concentration of GH was higher in the goats than in the ewes for the whole lactation, with the exception of the second sampling day (15 DIM). The values of goats had a very high concentration at 49 DIM, whereas in ewes GH concentration reached the peak at 35 ± 11 DIM (Figure 5A). For both species, the values were higher in early lactation than mid lactation. In goats, after 94 DIM, GH level increased until 113 DIM and thus decreased until 134 DIM. In contrast, insulin level increased during lactation in both species ($P < 0.0001$; Figure 5B) even though this trend was most pronounced in the ewes. The IGF-I concentrations (Figure 5C) were not affected by species.

The effect of period was significant for all variables considered. Except for plasma glucose, the effect of species × period interaction was significant for all variables considered, probably due to the change of the diet in mid lactation.

DISCUSSION

Evolution of Feed Intake, Milk Production, and Body Reserves

The diets were supplied ad libitum and, for their composition, probably did not impose any physical constraints to the daily DMI of the animals, which was likely regulated by their metabolic demand. The peak

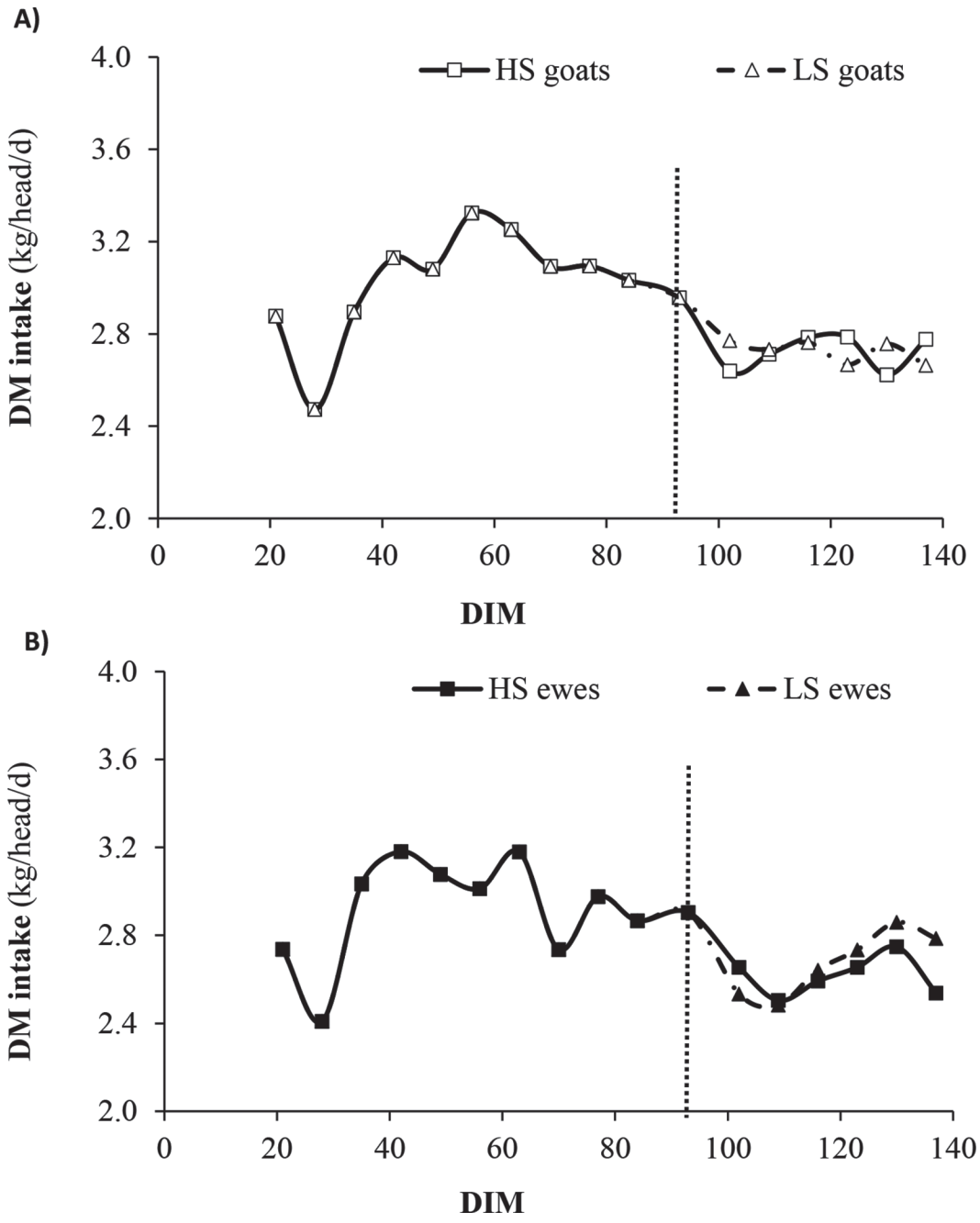

Figure 1. Evolution of group intake (kg/d of DM) of (A) Saanen goats and (B) Sarda ewes fed a high-starch (HS) diet from early lactation to 91 DIM and either an HS or low-starch (LS) diet from 92 DIM to end of the experimental period. The vertical bar at 92 DIM indicates the day of change of diet, in which both species were allocated to 2 dietary treatments.

of DMI was reached between 40 and 60 DIM, after which DMI decreased, in a pattern common to all dairy ruminants.

The pattern of milk production was in line with the lactation curves for ewes and goats described in the literature for these species. Because milk production was not measured in the first 45 d, no clear peak of lactation was evident, especially for the ewes. Indeed, dairy ewes often do not have this peak and decrease their milk production after parturition (Cappio-Borlino et al., 1997). Milk production was high in both species during the whole experiment. It is well known that

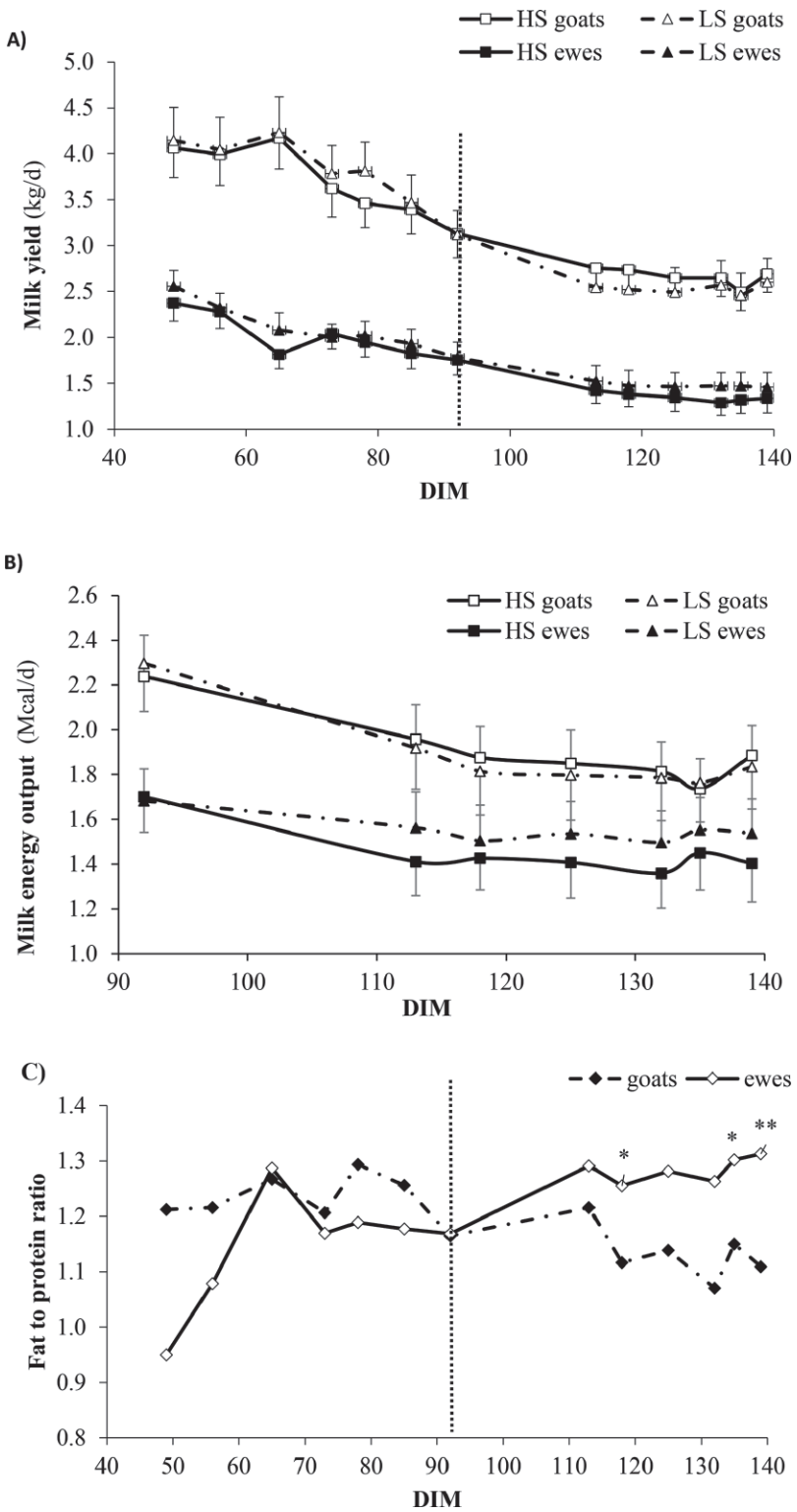

Figure 2. Evolution of (A) milk yield (kg/d) during the whole lactation, and (B) of milk energy output (Mcal/d) during the period of application of dietary treatments, (C) fat-to-protein ratio during the whole lactation, in Sarda ewes and Saanen goats fed a high-starch (HS) diet from early lactation to 91 DIM and HS and low-starch (LS) diets from 92 DIM to end of the experimental period. The vertical bar at 92 DIM in (A) indicates the day of change of diet, in which both species were allocated to 2 dietary treatments. From 92 DIM to the end of the experimental period, when HS and LS diets were compared, the effect of diet was significant ($P = 0.011$) only within goats for milk yield (A) and in both species for milk energy output (goats: $P = 0.025$, ewes: $P = 0.008$; B). All data are presented as mean ± SEM; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$, $\#0.10 \geq P > 0.05$ at the respective time point.

dairy goats of the Saanen breed have very high milk production and persistency. The milk production values for the Sarda ewes used in this experiment were higher than that usually observed for this breed (Carta et al., 2009; Ferro et al., 2017), because the ewes selected for the trial used all had high genetic merit, being part of the selection flock of the Sarda breed.

Interestingly, it was clear that stage of lactation and milk yield markedly affected the fat-to-protein ratio in ewes but not in goats. Indeed, the milk fat-to-protein ratio was low in sheep in early lactation, due to the low milk fat content when milk production was high. This situation changed progressively during the lactation, with milk fat and protein concentrations increasing as

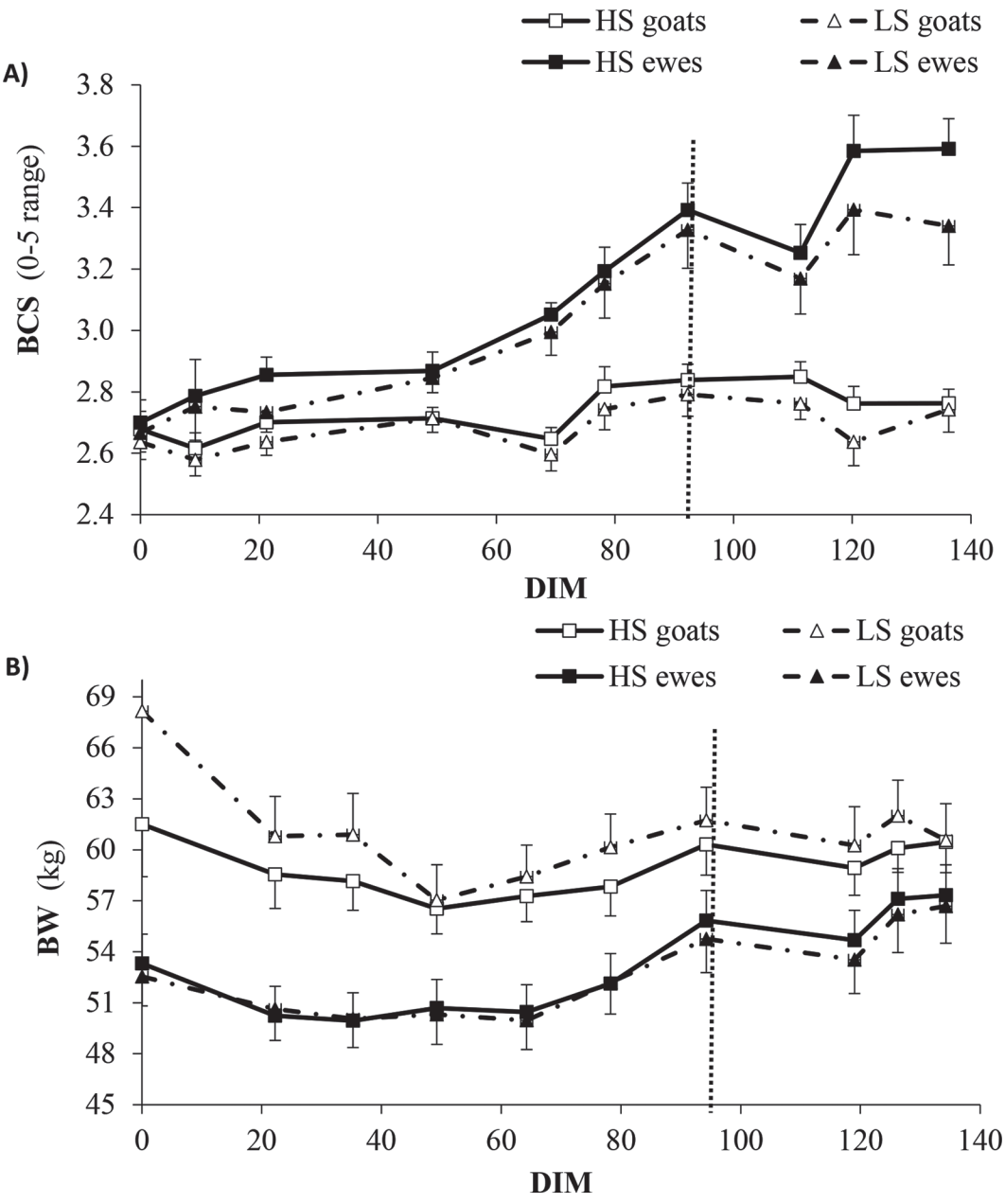

Figure 3. Evolution of (A) BCS (0–5 range) and (B) BW (kg) in Sarda ewes and Saanen goats fed a high-starch (HS) diet from early to 91 DIM and either HS and low-starch (LS) diets from 92 DIM to end of the experimental period. The vertical bar at 92 DIM indicates the day of change of diet, in which both species were allocated to the 2 dietary treatments. From 92 DIM to the end of the experimental period, when HS and LS diets were compared, the effect of diet on BCS was significant ($P = 0.008$) only within sheep (A), the effect of diet on BW was not significant in goats or ewes.

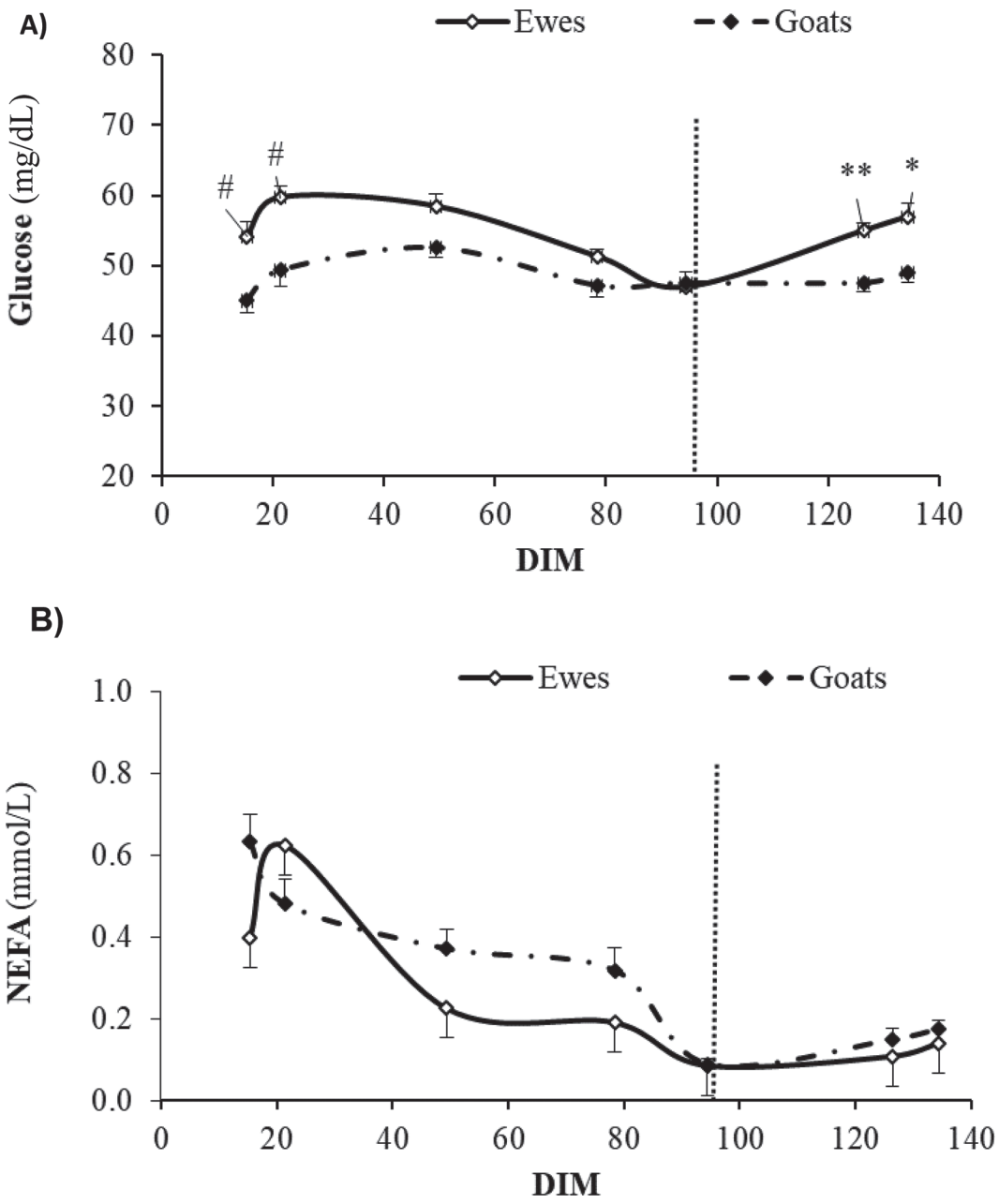

Figure 4. Evolution of plasma concentration of (A) glucose (mg/dL), and (B) nonesterified fatty acids (NEFA) (mmol/L), in Sarda ewes and Saanen goats fed a high-starch (HS) diet from early lactation to 91 DIM and either HS and low-starch (LS) diets from 92 DIM to the end of the experimental period. The vertical bar at 92 DIM indicates the day of change of diet, in which both species were allocated to the 2 dietary treatments. The effect of diet was never significant, thus data after the vertical bar are shown as the mean (within species) of the 2 diets. All data are presented as mean ± SEM; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$, # indicates $0.10 \geq P > 0.05$ at the respective time point.

milk production decreased. In contrast, in goats, the milk fat-to-protein ratio and fat and protein concentrations were very stable during the whole lactation and were not much affected by stage of lactation or by milk yield. We do not have a clear explanation for this large species difference.

An important finding of this work is that the applications of the differentiated diets after DIM 92 caused important variations in milk yield. The goats produced more milk with the HS diet than the LS diet. In the ewes, milk production did not differ but daily milk energy output (Figure 2B) was significantly higher with

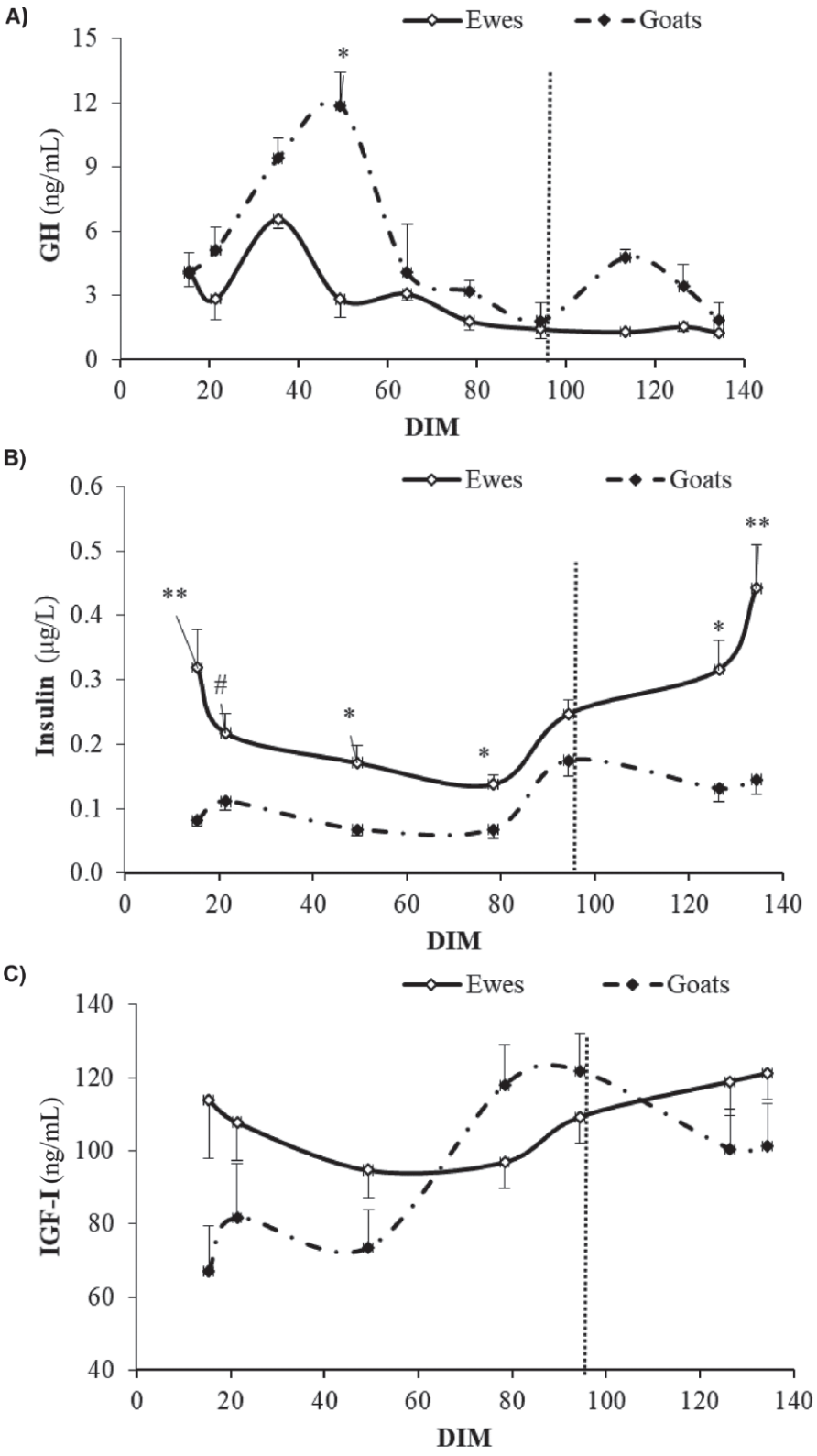

Figure 5. Evolution of plasma concentration of (A) growth hormone (GH; ng/mL), (B) insulin (µg/L), and (C) IGF-I (ng/mL), in Sarda ewes and Saanen goats fed a high-starch (HS) diet from early lactation to 91 DIM and either HS and low-starch (LS) diets from 92 DIM to end of the experimental period. The vertical bar at 92 DIM indicates the day of change of diet, in which both species were allocated to the 2 dietary treatments. The effect of diet was never significant, thus data after the vertical bar are shown as the mean (within species) of the 2 diets. All data are presented as mean ± SEM; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$, # indicates $0.10 \geq P > 0.05$ at the respective time point.

the LS diet. The BCS did not differ between HS- and LS-fed goats, whereas in ewes, BCS was significantly higher for those fed the HS diet.

These findings agree with other experiments on dairy sheep. Indeed, in mid-lactating dairy ewes, some experiments showed that diets rich in highly digestible fiber (e.g., high content of beet pulps or soybean hulls) increased milk production compared with high-starch diets (Cavani et al., 1990; Cannas et al., 1998, 2002, 2004, 2013; Bovera et al., 2004; Cabiddu et al., 2006), and in some case also stimulated body fat deposition (Cavani et al., 1990; Cannas et al., 2002, 2004, 2013). Conversely, a positive effect of highly digestible fiber in mid lactation has not been observed in goats, which responded positively to HS diets in this lactation stage (Cannas et al., 2007; Ibáñez et al., 2015).

Overall, these differences indicate a different response to the same nutrients between the 2 species, as also found in Sarda ewes fed similar HS and LS diets in pregnancy (no difference in baseline glucose plasma levels; Lunesu et al., 2020). In terms of metabolic parameters, no differences due to the dietary treatments were found within species; thus, only the differences between species were taken into account.

Glucose

In this study, glucose concentration was significantly lower in goats than in ewes. Considering that blood glucose is the most important lactose precursor (Oddy et al., 1985; Bell and Bauman, 1997), and that the mammary gland is identified as a glucose-dependent organ (Zhao and Keating, 2007), the lower blood glucose concentration observed in goats compared with ewes can likely be attributed to greater utilization by the mammary gland in goats than in ewes. Indeed, due to their much higher milk production, the goats in the experiment had a much higher daily lactose output than the ewes (on average, 114 vs. 63 g/d of lactose, for goats and ewes, respectively). In other words, the lower glycemic value observed in the goats compared with the ewes could be due to goats' use of glucose to sustain milk production, which requires a large amount of lactose. The amount of glucose uptake by the mammary gland, as reported by De Koster and Opsomer (2013), is the result of intensive genetic selection. In fact, milk production causes an important drain of glucose (Veerkamp et al., 2003). Thus, the lowest plasma glucose level observed in the goats could be linked, indirectly, to their likely highest genetic selection in accordance to what was suggested previously for dairy cows (Veerkamp et al., 2003). For the same motivation, it is possible that the ewes, likely subjected to less intense genetic selection for milk production, used more glucose for lipogenesis and body reserves accumulation compared with goats.

Nonesterified Fatty Acids

The higher NEFA content (mean value of the whole period; 15–134 ± 11 DIM) observed in goats compared with ewes confirmed the important energy requirement of this species to sustain milk production, probably achieved in part through the mobilization of body reserves when the glucose level decreased (Veerkamp et al., 2003). The pattern of NEFA was specular, as expected, to that of BCS and varied with the change of energy balance, confirming that NEFA can be considered good indicators of energy balance (Khan and Ludri, 2002; Adewuyi et al., 2005).

The highest plasma NEFA level observed in goats could be linked indirectly to their highest genetic selection in accordance to what suggested previously for dairy cows (Veerkamp et al., 2003), even though some studies did not find a relationship (Westwood et al., 2000; Roche et al., 2006). Compared with goats, ewes seem to be more prone to favor body fat deposition than fat mobilization, as observed in some comparative studies between the 2 species (El Khidir et al., 1998; Tshabalala et al., 2003; Sen et al., 2004).

Growth Hormone

The concentration of GH was higher in the goats than in the ewes during the most of the lactation. The values of goats had a very high concentration peak at 49 DIM, whereas in ewes, GH concentration peaked earlier, at 35 ± 11 DIM (Figure 5A). Because it has been reported that GH is secreted in pulses with a frequency of approximately 6 h in sheep, cattle, and deer, and that there is a secretory burst around the anticipated time of meal supply but no other secretion for about an hour after feeding (McMahon et al., 2001), the samples were taken just before the morning meal to limit the effects of pulsatility, at the same time and day in both species. Indeed, Kasuya (2016), in a review dedicated to the secretory pattern of GH in cattle, highlighted that in full-fed cattle, there is high synchronicity of the pattern based on the distance from the meal.

Sequential blood sampling at 30, 60, 120, 180, and 240 min after the morning meal also showed the species differences and the lack of dietary effects reported in our study (Lunesu et al., 2019). The literature in other papers (e.g., Rhoads et al., 2004; Accorsi et al., 2005) measured the evolution of GH over the lactation (or other physiological stages) by taking samples once per day. So even if the study of this hormone would be more detailed with frequent sampling, the results obtained

allow us to evaluate the relevance of this hormone in the nutrient partitioning in lactation.

The highest values of GH observed in the goats in our study are probably associated with the higher milk yield of this species compared with that of ewes measured in our experiment, confirming the important galactopoietic activity of this hormone (Peel and Bauman, 1987; Neville et al., 2002; Baumgard et al., 2017). Probably, the highest value of GH observed in goats can be due to the genetic selection for milk production to which Saanen goats have been subjected, in analogy to what observed previously in dairy cows (Kazmer et al., 1986; Veerkamp et al., 2003; Weber et al., 2007). The high GH concentration occurs as physiological adaptation to sustain lactation and stimulating lipolysis and glucose and acetate partitioning from peripheral tissues to the mammary gland (Hart, 1983; Davis and Collier, 1985). According to its lipolytic effect, increasing the amount of reserves mobilized, GH could be responsible for the higher NEFA content observed in the goats than in the ewes of this experiment.

As reported by Hart (1983), the nutrient partitioning toward the mammary gland driven by GH occurs only if milk production is sufficiently high, whereas the effects are limited if the animals are not as productive. In our experiment, the pattern of GH was in accordance to what reported in the literature. Indeed, GH levels are high in early lactation and tend to decrease as the lactation progresses and with the associated reduction of milk production (Cannas et al., 2002; Petitclerc et al., 2000). In particular, the high values of GH in early lactation probably caused an insulin-resistant status that helped to drive nutrients toward the mammary gland, according to the inhibition of the insulin lipogenic action caused by the high GH level (Bauman and Vernon, 1993; Bell and Bauman, 1997). As lactation advanced, GH concentration was decreased and milk production was reduced, in association with insulin sensitivity status. However, to our knowledge, there are no reports describing the evolution of GH during the whole lactation of dairy ewes and goats; the information available is fragmented to specific stages and short periods, as reported by Cannas et al. (2002).

Insulin

Insulin concentration was significantly higher in the ewes than in the goats, and it increased as milk production decreased, similarly to what has been observed previously in dairy cows (Bell and Bauman, 1997; Sasaki, 2002; Fiore et al., 2014). Similar differences between species were detected in the postprandial test carried out by Lunesu et al. (2019) using the same animals and diets at 165 DIM, as already explained. Taking for granted that insulin is the primary anabolic coordinator of nutrient partitioning, which drive nutrients toward peripheral tissues and increases cellular glucose uptake (Baumgard et al., 2016), these results suggest that an anabolic pathway prevails in lactating ewes, especially in mid lactation. This helps ewes to restore body reserves mobilized in early lactation, according to the positive association between blood insulin level and body fat deposition (Rosi et al., 2009). Insulin metabolism regulation in dairy ewes is also regulated by mechanisms of fetal programming (Lunesu et al., 2020). This could suggest a high sensitivity of Sarda ewes in mid-late lactation to a short-term supply of glucogenic precursors (glycerol and propylene glycol), resulting in a marked increase in the plasma level of glucose and insulin, which are positively associated with improved oocyte developmental competence (Berlinguer et al., 2012) but negatively associated with milk production, lactose synthesis, and urea and NEFA plasma concentration (Porcu et al., 2018). All the above concur with the hypothesis that Sarda ewes may need a high level of insulin and glucose and a more pronounced anabolism to ovulate and hence, to successfully mate during lactation in late spring or early summer. In contrast, dairy goats presented a metabolic status more inclined toward a catabolic pathway able to sustain milk production, even in mid lactation. Moreover, the lower insulin concentration in goats can be considered as a physiological adaptation to support lactation in this species, as suggested by Baumgard et al. (2017). Possible explanations of these differences between species and breeds can be linked to a higher intensity of genetic selection for milk production in Saanen goats compared with Sarda ewes, but we are not aware of any specific comparative research in this sense.

In ewes, the marked insulin increase after the peak of lactation was associated with concomitant marked body reserves accumulation, which was significantly higher in the HS ewes compared with LS ewes. A similar pattern occurred in the goats, even though both the insulin increases and the body reserves increases were milder than in the ewes. In addition, BCS did not differ between HS and LS goats.

Insulin-Like Growth Factor I

The IGF-I concentrations differed numerically, being higher in sheep than in goats, but they were significantly and markedly higher in sheep than goats in the postprandial test carried out by Lunesu et al. (2019) using the same animals and diets of our experiment but at 165 DIM. The IGF-I values were substantially lower in goats than in ewes in the first 2 mo of lactation but were more similar later on, consistent with hte litera-

ture that also reported IGF-I is low in high-genetic-merit cows (Weber et al., 2007), due to a physiological adaptation that occurs to support lactation (Baumgard et al., 2017).

The IGF-I values tended to increase during lactation as the energy balance became increasingly positive (effect of period: $P = 0.0005$) in accordance with the increase in insulin and decrease in NEFA and GH. Thus, IGF-I was probably involved in the partitioning of nutrients toward body fat deposition rather than the mammary gland. This is in accordance with a previous study that evidenced insulin-complementary activity of this hormone, even though IGF-1 secretion is controlled by GH, which has a catabolic effect (Veerkamp et al., 2003).

CONCLUSIONS

This work was developed to find a biological reason that would explain the previously reported different behavior in the use of carbohydrates (starch and highly digestible fiber) between lactating dairy goats and ewes. Overall, it appeared that Saanen goats had, throughout the period studied, a hormonal status (high GH and low insulin concentration) that favored the partition of dietary energy for milk production, whereas the Sarda ewes showed a hormonal status (low GH and high insulin concentration), particularly pronounced in mid lactation, more prone to partition dietary energy for body reserves accumulation. Because in this study no direct effects of the dietary starch level on the metabolic hormonal status were observed, it is likely that, due to their inherent different hormonal status, Saanen goats used high-starch diets in mid lactation to maintain high levels of milk production, whereas Sarda ewes used it for boosting body reserves accumulation. Results of this simultaneous comparison under the same feeding and background conditions clearly showed that Saanen goats and Sarda dairy ewes have a different hormonal control of energy partitioning during lactation, with ewes being more insulinemic, especially during mid lactation, compared with dairy goats. These differences have important implications in terms of optimal dietary carbohydrate sources and concentrations during lactation, which likely differ between the 2 species, especially in mid and late lactation.

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