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Bérengère Laporte Laporte-Broux, Sabine Roussel, Andrew A. A. Ponter, Julien J. Perault, Pascale Chavatte-Palmer, Christine Duvaux-Ponter

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Short-term effects of maternal feed restriction during pregnancy on goat kid morphology, metabolism, and behavior[1]

B. Laporte-Broux,*†‡§[2] S. Roussel,*† A. A. Ponter,‡§ J. Perault,*†‡§ P. Chavatte-Palmer,‡§ and C. Duvaux-Ponter*†

*INRA, UMR 791 Modélisation Systémique Appliquée aux Ruminants, 16 rue Claude Bernard, F-75231 Paris cedex 05, France; †AgroParisTech, UMR 791 Modélisation Systémique Appliquée aux Ruminants, 16 rue Claude Bernard, F-75231 Paris cedex 05, France; ‡INRA, UMR 1198 Biologie du Développement et Reproduction, F-78350 Jouy-en-Josas, France; and §ENVA, UMR 1198 Biologie du Développement et Reproduction, 7 avenue du Général de Gaulle, F-94704 Maisons-Alfort cedex, France

ABSTRACT: Morphometric, metabolic, and behavioral modifications were studied in goat kids after maternal feed restriction during the last one-third of pregnancy. At birth, only kids from twin and triplet litters were studied [n = 40 kids born to control dams (CONT) and n = 38 born to restricted dams (REST)] and only males thereafter (n = 13 CONT and 15 REST kids) until slaughter at 6 wk of age. Kids born to restricted goats had a smaller abdominal girth at birth ($P < 0.01$) and tended to have a smaller body mass index ($P = 0.10$) and a smaller density index ($P = 0.09$) than kids born to CONT goats. Male REST kids had a lighter birth weight ($P = 0.03$) than male CONT kids, but no differences (all $P > 0.10$) were found for BW and morphometric measurements thereafter. Decreased NEFA concentrations suggested that male REST kids mobilized their body reserves less than CONT kids at birth ($P < 0.01$). No modifications in drinking tests at 3 and 5 wk of age were observed, or in feeding behavior and emotional reactivity at 5 wk of age (all $P > 0.10$). In conclusion, maternal feed restriction in the last one-third of pregnancy resulted in a decrease in birth size, but male kids rapidly caught up, and there were no changes in behavior, morphology, or metabolism during rearing.

Key words: emotional reactivity, feeding behavior, fetal programming, goat, maternal feed restriction, metabolism

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INTRODUCTION

Maternal feed restriction during pregnancy can have various effects on offspring development and in adult life, depending on timing (Sinclair and Singh, 2007), duration (McCrabb et al., 1992), intensity of restriction (Russel et al., 1977), sex (Grigore et al., 2008), and litter size (Rumball et al., 2008). During late pregnancy, feed restriction was associated with insulin resistance and increased adiposity in human and animal offspring (Sinclair and Singh, 2007; Symonds et al., 2007).

Changes in offspring feeding behavior after maternal feed restriction in late pregnancy could be expected in some species. The hypothalamus is the main brain structure involved in the control of feed intake, and its maturation mainly occurs in late gestation in sheep (Matthews and Challis, 1996). Warnes et al. (1998) showed an increase in the amount of neuropeptide Y mRNA, an orexigenic neuropeptide, in near-term fetal sheep from late-gestation-restricted dams. Studies in rodents born to pregnancy and lactation-restricted dams showed changes in neuropeptide expression associated with hyperphagia (Orozco-Sólis et al., 2009) and changes in feed preference (Bellinger et al., 2004, 2006; Bellinger and Langley-Evans, 2005). Moreover, maternal feed restriction in the ruminant can cause intrauterine growth restriction (Anthony et al., 2003), which is associated with very light birth weight. Feed intake in very light birth weight lambs was greater in

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[2]Corresponding author: berengerelaporte@yahoo.fr
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proportion to BW when fed ad libitum, compared with heavier birth weight lambs (Greenwood et al., 1998).

Emotional reactivity can modify feeding behavior (Torres and Nowson, 2007) and is increased in 18-mo-old lambs born to early-pregnancy-restricted dams (Erhard et al., 2004). However, the interaction between emotional reactivity and feeding behavior has never been taken into consideration when studying the effects of restriction during pregnancy on feeding behavior.

Because structures involved in emotional reactivity and feeding behavior can be programmed in utero and the maturation of the hypothalamus mainly occurs in late pregnancy, we hypothesized that maternal feed restriction in the last one-third of pregnancy could change feeding behavior and emotional reactivity in kids. The consequences of maternal feed restriction on growth, composition, metabolites and hormones associated with energy metabolism, and morphology were also evaluated.

MATERIALS AND METHODS

The present study was carried out according to French legislation on animal experimentation (code rural: articles R214-87 to R214-94) in line with the European Convention for the Protection of Vertebrates used for Experimental and other Scientific Purposes (European Directive 86/609). The scientist in charge of the experiments was licensed to perform experiments on animals, and the staff who applied the experimental procedures had attended a special course approved by the French Ministry of Agriculture.

Animals and Procedures

Pregnant Goats. Sixty multiparous gestating Saanen and Alpine dairy goats were divided into 2 groups according to BW, BCS, kid sire, and breed. The goats were synchronized before mating to ensure birth within a period of 10 d. At 90 d of gestation, each group (control, n = 13 Alpine and n = 17 Saanen; and restricted, n = 14 Alpine and n = 16 Saanen) was divided into 2 subgroups on the basis of BW (15 heavy goats and 15 light goats) to reduce aggression between light and heavy restricted goats at the feeding trough and to better adjust the amount of feed to BW. Both control subgroups were fed ad libitum a total mixed ration (**TMR**) allowing 5% orts. Each feed restricted subgroup was pair-fed to the corresponding control subgroup and received a proportion of the amount given to the pair-fed control subgroup. Light control subgroup (mean BW: 61 ± 1.6 kg) was pair-fed to light restricted subgroup (mean BW: 62 ± 1.4 kg), and the heavy control subgroup (mean BW: 82 ± 2.5 kg) was pair-fed to the heavy restricted subgroup (mean BW: 83 ± 2.5 kg). The amount of feed given to the restricted subgroup was calculated from the amount of feed given to the control subgroup the previous week. The composition of the TMR was modified in the last weeks of gestation to take into account the proportionally faster increase in protein requirements compared with energy (Table 1). The mineral and vitamin mix included in the TMR contained 180 $g{\cdot}kg^{-1}$ of phosphorus, 90 $g{\cdot}kg^{-1}$ of calcium, 60 $g{\cdot}kg^{-1}$ of magnesium, 30 $g{\cdot}kg^{-1}$ of sodium, 600,000 $IU{\cdot}kg^{-1}$ of vitamin A, 150,000 $IU{\cdot}kg^{-1}$ of vitamin D_3, 1,200 $mg{\cdot}kg^{-1}$ of vitamin E, 1,000 $mg{\cdot}kg^{-1}$ of copper, 7,000 $mg{\cdot}kg^{-1}$ of zinc, 6,000 $mg{\cdot}kg^{-1}$ of manganese, 100 $mg{\cdot}kg^{-1}$ of iodine, 60 $mg{\cdot}kg^{-1}$ of cobalt, and 40 $mg{\cdot}kg^{-1}$ of selenium). Propylene glycol (Propypact, Difagri Picot SA, Saint-Hilaire-de-Loulay, France) was added to the TMR (40 $g{\cdot}d^{-1}$ per goat) to avoid pregnancy toxemia that can occur in late-pregnancy feed restriction (Rook, 2000) and can result in death. When 3 goats presented symptoms of toxemia in the restricted subgroups, for ethical reasons it was decided to increase the amount of feed progressively. Therefore, each restricted subgroup received 50% of the amount of feed given to their pair-fed control subgroup for 4 wk, 60% for 1 wk, 70% for 1 wk, and 80% the last 2 wk of pregnancy.

Goats were group-fed and feed was offered twice daily at 0700 and 1400 h. The restricted goats were restrained in a neck-lock for 30 min during feeding to avoid competition at the trough and to make sure that all goats were able to eat. All groups had free access to water and salt licks. The restricted goats received barley straw (NE: 3.1 $MJ{\cdot}kg^{-1}$ of DM; true protein digested in the small intestine: 24 $g{\cdot}kg^{-1}$ of DM; and DM: 880 $g{\cdot}kg^{-1}$) ad libitum after feeding to reduce as much as possible of the psychological stress due to feed restriction (Mason, 1971).

Among the 60 goats, 5 control goats and 8 restricted goats (of the latter 4 became toxemic) were removed because of abortion or health problems. The 47 remaining goats gave birth to single (n = 12), twin (n = 21), triplet (n = 12), and quadruplet (n = 2) litters. Only the kids born to healthy twin- and triplet-bearing does were studied thereafter. Gestation length, DMI, BW loss, and glucose and NEFA plasma concentrations of the 33 corresponding goats (n = 11 Saanen and n = 6 Alpine for control goats; and n = 10 Saanen and n = 6 Alpine for feed-restricted goats) were measured at the beginning of the restriction period (90 d of pregnancy), during the feed restriction period and the last week of pregnancy.

Kids. At birth, 78 kids, among them 40 control kids (**CONT**; 26 females and 14 males) and 38 restricted kids (**REST**; 21 females and 17 males) born to 33 goats were studied. Thereafter, females were kept elsewhere for herd renewal and were, therefore, not included in the rest of the study. From 1 wk of age until the end of the experiment, 28 male kids, among them 13 control kids (8 twin and 5 triplet litters; 7 Alpine and 6 Saanen) and 15 restricted kids (9 twin and 6 triplet litters; 4 Alpine and 11 Saanen) were studied. At 6 wk of age, for practical reasons, only 20 males could be slaughtered (10 restricted and 10 control). They were chosen to balance treatment and breed, and only 1 male per

Table 1. Composition and energy content of the diet given to feed-restricted and control goats starting from 90 d of pregnancy

Item	−8 to −4 wk	−4 to −2 wk	−2 wk to parturition
Composition, g·kg^{-1} of DM			
Sugar-beet pulp	350	300	300
Grass hay	250	250	250
Lucerne hay	290	290	290
Protein concentrate	0	50	100
Barley	100	100	50
Mineral and vitamin mix	10	10	10
Nutrient, ·kg^{-1} of DM			
NE, MJ	5.7	5.6	5.5
PDI,[1] g	69	73	76
CP, g	112	116	120
Crude fiber, g	292	285	287
NDF, g	493	452	479
Calcium, g	9.0	8.5	8.7
Phosphorus, g	2.0	2.3	2.4

[1]PDI = true protein digested in the small intestine.

litter was kept to avoid an effect of the dam. If more than 1 male was available per litter, it was chosen randomly.

At birth, kids were immediately removed from their dam and ear-tagged. Two meals of good quality pooled colostrum were given ad libitum on d 1, and a 150 g·kg^{-1} fresh weight diluted milk replacer (235 g·kg^{-1} of protein, 240 g·kg^{-1} of fat, 70 g·kg^{-1} of ash, 3 g·kg^{-1} of cellulose, 50,000 IU·kg^{-1} of vitamin A, 2,000 IU·kg^{-1} of vitamin D_3, 85 mg·kg^{-1} of vitamin E, 10 mg·kg^{-1} vitamin B_1, 11.5 mg·kg^{-1} of vitamin K_3, and 750 mg·kg^{-1} of vitamin C) was given ad libitum the next 3 d. On d 5, the kids were identified with paint and placed in 1 of 3 experimental pens (2 × 2.5 m). In each pen, 9 or 10 restricted and control kids were mixed, and there was a maximum of 4 d between the youngest and the oldest kid.

A camera was placed above each pen and linked to a time-lapse video recorder to allow 24-h recording of suckling activity. A neon light (36 W) was fitted to the ceiling and was activated continuously to allow behavior to be recorded during the night. The intensity of the light was weak to not disturb kid behavior.

BW, Morphometric, and Slaughter Measurements

Body weight was recorded at birth and weekly until 6 wk of age. Crown-rump length (distance between crown and sacrococcygeal joint), height at withers, heart girth (taken just behind the forelimbs), abdominal girth (circumference of the abdominal cavity taken just in front of the hindlimbs), and femoral length were measured with a flexible tape on standing kids at birth and once each week before feeding until 4 wk of age. Body mass index (**BMI**; BW/(crown-rump length)^2, kg·m^{-2}), density index (BW/crown-rump length, g·cm^{-1}) as used in swine (Johnson and Nugent, 2003), and ADG were calculated.

At 6 wk of age, after 12 h of fasting, kids were slaughtered by exsanguination after electronarcosis. Weights of liver, kidneys, adrenals, pancreas, forestomachs (rumen, reticulum, omasum), abomasum, thymus, brain, heart and lungs, and adipose tissue (perirenal, pericardiac, and omental tissue mass) were recorded after dissection. The total body fat was calculated as the sum of the 3 dissected adipose tissues.

Behavioral Tests and Measurements

In addition to the 24-h suckling activity, standardized tests were performed to measure suckling behavior as well as to test the emotional reactivity of the kids. All video files were encoded and analyzed using The Observer 5.0 Software System for Behavioral Research (Noldus Information Technology, Wageningen, the Netherlands).

Novel Arena Test. The novel arena test (Forkman et al., 2007) was performed in an open-sided shed (50 m away from the rearing pens) in a 4 × 3.2 × 1.5 m arena (width × depth × height) in 5-wk-old kids (a few days after other behavioral measurements). A starting cage, measuring 1.2 × 0.6 m, provided access to the arena. Each kid was carried by an experimenter from the rearing pen to the testing pen, gently placed in the starting cage, and released 30 s later into the arena using a sliding gate. The procedure was designed to ensure that the handling was standardized. The test lasted 3 min once the kid entered the arena. Time spent still (kid with 4 legs still), time spent sniffing (nose less than 5 cm from the floor or walls), and number of jumps and bleats were measured. This test was performed alternatively on 1 kid from each treatment between 0800 and 1200 h.

Novel Object Test. Immediately after the novel arena test (on the same day), the kid was placed in the starting cage (30 s) for a second test of 3 min in the same arena that contained a red polypropylene road hazard cone (0.4 × 0.7 m) placed on the floor against the wall opposite the entrance (Forkman et al., 2007). The same behavioral measurements as those in the novel arena test were conducted. Time spent sniffing the cone (nose less than 5 cm from the cone) was also recorded.

Drinking Test. Drinking tests were performed in a familiar pen at 3 and 5 wk of age (after suckling activity measurement and a few days before the arena and novel object tests). The test was performed in a pen (3 × 2 m) containing a bucket with a teat. The bucket was filled with milk replacer and fixed on the opposite wall from the entrance. A video camera was placed above the pen to videotape behavior. To familiarize the kids with the testing pen, kids from the same experimental pen were placed in the pen at 1700 h the day before the test and were allowed to drink for 2 h from the bucket. After removing the bucket, and leaving the kids overnight in the pen (12-h fasting), an open partition was added to keep all the kids on 1 side of the pen, near the entrance. The bucket filled with milk replacer was fixed on the wall, and each kid was individually placed in the part of the pen containing the bucket. This test was performed alternatively on 1 kid from each treatment between 0800 and 1200 h. The test ended when the kid spent 1 min without drinking. The bucket was weighed before and after the test. The percentage of time spent drinking, the amount of milk drunk, and the drinking rate (amount of milk drunk divided by the time spent drinking) were recorded.

Drinking Test After Isolation Acute Stress. This test was performed the next day using the same procedure and measuring the same variables as the previous test, except that kids were stressed before entering the testing pen by spending 20 min alone in a small cage with no visual contact with peers (0.95 × 0.57 × 0.33 m).

Suckling Activity. In each experimental pen, the kids had 24-h access to 2 individual stalls equipped with 1 teat each where they could drink milk replacer ad libitum through an automatic milk feeder. When feeding behavior was measured, an isotherm container containing warm milk replacer was connected to 1 teat and placed outside the pen on a weighing device connected to a computer that recorded container weight every 10 s. Suckling activity was videotaped over 24 h in the rearing pen at 5 wk of age. Time spent with a teat in the mouth per 24 h ($\mathbf{t_M}$) and number of suckling bouts per 24 h ($\mathbf{n_S}$) were recorded. A suckling bout begun when a kid took a teat in its mouth and ended when the kid released the teat. Mean duration of a suckling bout was calculated ($\mathbf{m_D} = t_M/n_S$). Correspondence between videotaped behavior and milk consumption was assessed using automatic weighing devices. The amount of milk consumed per 24 h and efficient suckling time per 24 h ($\mathbf{t_D}$) could be calculated for each kid. Efficient suckling time was the time during which the kid had a teat in the mouth while at the same time the amount of milk in the container decreased. Sometimes the kid had a teat in the mouth but did not drink. The percentage of efficient suckling time ($\mathbf{t_{DM}} = 100\ t_D/t_M$) was calculated.

Physiological Measurements

Blood samples (10 mL) were collected into heparinized tubes by jugular venipuncture and were immediately centrifuged at 3,000 × *g* for 10 min at 4°C to harvest plasma. Blood samples were taken from the 28 male kids within 1 h of birth (before colostrum feeding) and after 12 h of fasting at 1, 3, and 5 wk of age. Plasma was stored at −20°C until analysis. Leptin and insulin concentrations were measured at birth and at 5 wk of age. Glucose and NEFA concentrations were measured at birth, 1, 3, and 5 wk of age.

Biological Assays

Plasma concentrations of leptin were quantified using double-antibody leptin RIA procedures adapted from Delavaud et al. (2000). Leptin antisera (Ab 7137, antisera raised against recombinant ovine leptin in rabbits; Delavaud et al., 2000; 50 μL) was diluted 1:2,200 in a 0.01 *M* phosphate buffer, 0.15 *M* NaCl, pH 7.1 containing 0.01 *M* EDTA, 0.1% gelatin, 0.01% sodium azide, 0.025% Tween 20, and 1% normal rabbit serum. Both standard and sample tubes were incubated with antisera (final dilution: 1:17,600) for 24 h at room temperature (20°C). After an initial incubation in 300 μL, 100 μL of ^{125}I-ovine leptin (diluted in the same buffer without EDTA) was added, and incubation continued for an additional 24 h at room temperature. Assay sensitivity was 1 ng·mL^{-1}, and the intraassay CV was 4%.

Insulin concentrations were determined using a RIA rat insulin kit (Millipore, Molsheim, France; 100% of specificity for sheep insulin). Assay sensitivity was 0.1 ng·mL^{-1}. Intraassay CV was 9.7%, and interassay CV was 14%.

A Cobas Mira S apparatus (La Roche & Co., Diagnostics Division, Basel, Switzerland) was used to measure plasma glucose (hexokinase reaction) and plasma NEFA (NEFA C, ACS-ACOD method). The intraassay CV were 2 and 1% for glucose and NEFA, respectively. The interassay CV were 8.7 and 3.4% for glucose and NEFA, respectively.

Statistical Analysis

All data were analyzed using the MIXED model procedure (SAS Inst. Inc., Cary, NC).

For goats, the following model was used:

$$Y_{ijk} = \mu + T_i + L_j + B_k + \varepsilon_{ijk},$$

where Y_{ijk} represents the tested variable, μ represents the overall mean, T_i is the fixed effect of the treatment i (control and feed-restricted), L_j is the fixed effect of the litter size j (twins or triplets), B_k is the fixed effect of the breed k (Alpine or Saanen), and ε_{ijk} is the residual error.

For kids, the following models were used:

$$(1)\ Y_{ijkl} = \mu + T_i + B_j + S_k + TS_{ik} + D_{l/i} + \varepsilon_{ijkl}, \text{ and}$$

$$(2)\ Y_{ijm} = \mu + T_i + B_j + P_m + \varepsilon_{ijm}.$$

Model (1) was used to analyze birth data (males and females) and model (2) for the other variables. Body weight was added as a covariate except for BMI, ADG density index, and BW. For these variables, the fixed effect of the litter size j (twins or triplets) and the fixed effect of the interaction between treatment and litter size were taken into account. In models (1) and (2), Y_{ijkl} and Y_{ijm} represent the tested variable (at birth and the following weeks, respectively), successively: morphometry and growth (BW, crown-rump length, height at withers, heart girth, abdominal girth, femoral length, BMI, density index, ADG, organ and tissue weight), behavior (time spent still, time spent sniffing, time spent sniffing the cone, number of jumps, number of bleats, amount of milk drunk and drinking rate in drinking tests, amount of milk, percentage of efficient suckling time, mean duration of a suckling bout, time spent with a teat in the mouth), and metabolism (leptin, insulin, glucose, and NEFA concentrations). All variables were measured at birth and during the following weeks except behavioral variables (only measured a few weeks after birth). The μ represents the overall mean, T_i is the fixed effect of the treatment i (CONT or REST), B_j is the fixed effect of the breed j (Alpine or Saanen), S_k is the fixed effect of the sex k (male or female), P_m is the fixed effect of the rearing pen m (1, 2, or 3), and TS_{ik} represents the interactions between treatment and sex. The random effect of the dam l ($D_{l/i}$) was taken into account, and ε_{ijkl} and ε_{ijm} are the residual errors.

Transformations were used when the assumptions of homogeneity of variance and normal distribution of the residuals were not verified. Reverse transformation [1/(x + 1)] for abdominal girth and mean duration of a suckling bout (24 h suckling activity) were used at birth and 3 wk of age, respectively. All data are presented as least squares means ± pooled SEM. Differences were considered as significant when $P < 0.05$ and a trend when $0.05 \leq P < 0.10$.

RESULTS

Pregnant Goats

Among the 47 pregnant goats, light subgroups ate on average 1.9 and 1.1 kg of DM·d^{-1} (control and restricted goats, respectively; straw not included) and heavy subgroups ate on average 2.3 and 1.5 kg of DM·d^{-1} (control and restricted goats, respectively; straw not included) during the feed restriction period. Straw consumption was estimated as 0.4 kg of DM·d^{-1}. Restricted dams were, therefore, provided with around 70% of the energy given to the control goats between 90 d of gestation and parturition.

No difference in gestation length was observed between control and restricted goats (151 vs. 152 ± 0.6 d, respectively). At the start of the experiment, there were no differences in BW between control and restricted goats (74 vs. 73 ± 4.2 kg). The 33 restricted goats from which male kids were included in the experiment lost 8.2% BW between the start of feed restriction and 24 h after birth, whereas control goats lost 1.3% BW (−6.7 vs. −0.3 ± 1.57 kg, $P < 0.001$).

At 90 d of pregnancy, NEFA concentrations were 0.11 vs. 0.15 ± 0.045 mM in feed-restricted and control goats, respectively. At 90 d of pregnancy, glucose concentrations were 3.32 vs. 3.18 ± 0.084 mM, in feed-restricted and control goats, respectively. During the feed restriction period, NEFA concentrations increased more ($P < 0.001$, Figure 1), and glucose concentrations decreased more in restricted goats than in control goats ($P = 0.02$, Figure 1).

There was an effect of litter size: triplet-bearing goats lost more BW than twin-bearing goats ($P = 0.05$). There was a trend for NEFA concentrations to be greater in triplet-bearing goats compared with twin-bearing goats during the first one-half of the feed restriction period ($P = 0.09$), and for the whole feed restriction period, NEFA concentrations were greater in triplet-bearing goats compared with twin-bearing goats ($P = 0.04$).

Kids

Morphometric measurements at birth are summarized in Table 2 for the 78 male and female kids. Kids born to feed-restricted dams had a smaller abdominal girth than control kids ($P = 0.05$, Table 2). They

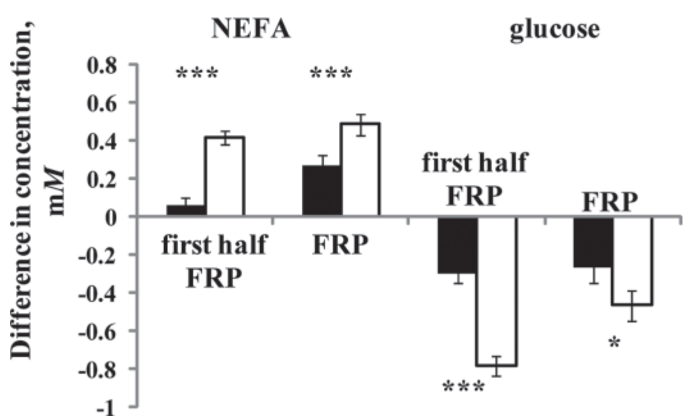

Figure 1. Differences in plasma NEFA and glucose concentrations during the first 4 wk of the feed restriction period (FRP) and during the whole FRP (from 90 d of pregnancy to parturition) in control (■, n = 17) and feed-restricted goats (□, n = 16). The control group was fed a total mixed ration (TMR) ad libitum for the last one-third of gestation and the feed-restricted group was given the same TMR, but the quantity corresponded to 50 (for 4 wk), 60 (for 1 wk), 70 (for 1 wk), and 80% (for 2 wk) of the amount given to the control group. Differences between treatments are shown, $^{*}P < 0.05$; $^{***}P < 0.001$.

Table 2. Morphometric variables of kids born to restricted dams (REST) during the last one-third of pregnancy or born to control dams (CONT), according to sex at birth[1,2]

	Treatment			Sex			*P*-value		
Item	CONT (n = 40)	REST (n = 38)	SEM	Male (n = 31)	Female (n = 47)	SEM	Treatment	Sex	Treatment × sex
Birth weight, kg	4.3	4.1	0.17	4.5	3.9	0.10	0.29	<0.0001	0.03
BMI,[3] $kg \cdot m^{-2}$	18.1	17.0	0.70	18.4	16.7	0.42	0.10	0.0004	0.98
Density index, $g \cdot cm^{-1}$	88.3	83.0	2.96	90.7	80.6	1.77	0.09	<0.0001	0.20
Abdominal girth,[4] cm	0.033 (29.7)	0.034 (28.0)	0.95	0.033 (28.9)	0.034 (28.7)	0.82	0.05	0.78	0.48
Heart girth, cm	34.4	35.1	0.53	35.3	34.1	0.42	0.18	0.008	0.05
Crown-rump length, cm	47.9	48.7	0.74	47.8	48.9	0.63	0.30	0.10	0.50
Femoral length, cm	12.4	12.2	0.57	12.1	12.5	0.28	0.80	0.24	0.06
Height at withers, cm	39.7	38.8	0.91	39.4	39.2	0.63	0.31	0.79	0.03

[1]The control goats were fed a total mixed ration (TMR) ad libitum for the last one-third of gestation and the feed-restricted goats were given the same TMR, but the quantity corresponded to 50 (for 4 wk), 60 (for 1 wk), 70 (for 1 wk), and 80% (for 2 wk) of the amount given to the control goats.

[2]Least squares means (back-transformed least squares means) and pooled SEM are presented.

[3]BMI = body mass index.

[4]1/(x + 1) transformation.

tended to have a lesser BMI and density index than control kids ($P = 0.10$ and 0.09, respectively; Table 2). The covariate BW influenced all variables; heavier kids had greater morphometric measurements than lighter kids ($P < 0.01$). There was an interaction between sex and treatment on birth weight; REST male kids were lighter than CONT male kids ($P = 0.03$), but there was no treatment difference in BW for females ($P = 0.84$). There was an interaction between sex and treatment on height at withers; REST female kids had a lower height at withers than CONT female kids ($P = 0.03$), but there was no difference in males ($P = 0.82$; Table 2). Male kids were heavier than females ($P < 0.0001$) and had a greater BMI ($P = 0.0004$) and density index ($P < 0.0001$; Table 2). Twins were heavier than triplets (4.6 vs. 3.9 ± 0.17, $P < 0.001$) and had a greater BMI (18.4 vs. 16.6 ± 0.61, $P = 0.006$) and density index (91.1 vs. 80.1 ± 2.93, $P < 0.001$).

Male Kids

Metabolic Variables. At birth, REST male kids had decreased NEFA concentrations compared with CONT male kids (Figure 2, $P = 0.003$). No treatment effect was observed for insulin concentrations (Figure 2) and leptin concentrations at birth (CONT: 78 ± 5.6 p*M* and REST: 82 ± 5.2 p*M*). No treatment effect was observed at 1, 3, and 5 wk of age on glucose and NEFA concentrations or on insulin (Figure 2) and leptin concentrations (CONT: 223 ± 21.2 p*M*; and REST: 199 ± 20.4 p*M*) at 5 wk of age. The covariate BW influenced glucose concentration at birth, 1 wk of age, and 3 wk of age ($P = 0.02$, 0.03, and 0.002, respectively) and influenced insulin concentration at birth ($P = 0.008$) and at 5 wk of age ($P = 0.05$); heavier offspring had greater plasma insulin and glucose concentrations than lighter offspring.

Behavioral Variables. No effect of treatment was observed on the percentage of time spent drinking, the amount of milk drunk, and the drinking rate in the drinking tests before and after an acute stress (all $P >$ 0.10, data not shown). Moreover, no treatment effect was observed on kid suckling behavior at 5 wk of age in the home pen; the amount of milk consumed per day, the time spent suckling, the percentage of efficient suckling time, and the mean duration of a suckling bout did not differ between CONT and REST male kids (Table 3). No effect of treatment was found on any behavioral variables measured in the novel arena and novel object tests (all $P > 0.10$, data not shown).

Morphometric and Slaughter Measurements. No effect of treatment was found on BW and on any of the morphometric measurements in the 28 males included in the experiment between 1 and 5 wk of age (all $P > 0.10$, data not shown). The covariate BW influenced all variables; heavier kids had greater morphometric measurements than lighter kids. There were no differences between CONT and REST kid daily BW gains between 1 and 5 wk of age (Figure 3, all $P > 0.10$). Twins remained heavier (all $P < 0.03$) than triplets between 1 and 5 wk of age. Body mass index tended to be greater at 1 and 4 wk of age ($P = 0.06$) and was greater at 2 wk of age ($P = 0.02$) in twins than in triplets (data not shown). Density index remained greater in twins than in triplets between 1 and 4 wk of age (all $P < 0.007$, data not shown). Daily BW gain was greater in twins than in triplets between 3 and 4 wk of age and between 4 and 5 wk of age (both $P <$ 0.03, data not shown).

No differences were found for any organ or tissue weight between CONT and REST kids at slaughter, but the covariate BW influenced all variables; heavier kids had heavier organs and tissues than lighter kids (all $P < 0.10$).

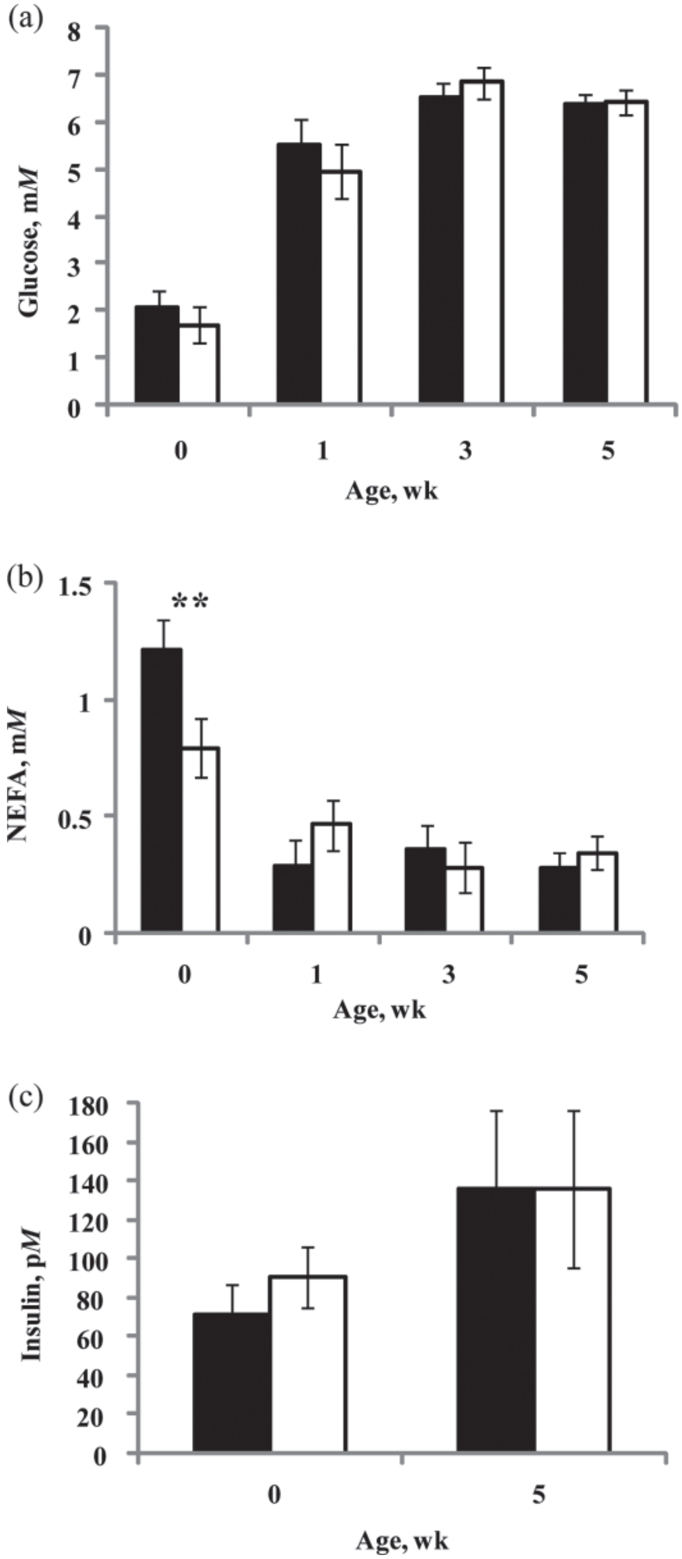

Figure 2. Plasma (a) glucose, (b) NEFA, and (c) insulin concentrations in male kids born to goats feed-restricted during the last one-third of gestation (□, n = 15) or to control dams (■, n = 13) at birth and at 1, 3, and 5 wk of age. The control goats were fed a total mixed ration (TMR) ad libitum for the last one-third of gestation and the feed-restricted goats were given the same TMR, but the quantity corresponded to 50 (for 4 wk), 60 (for 1 wk), 70 (for 1 wk), and 80% (for 2 wk) of the amount given to the control goats. Differences between treatments are shown, $^{**}P \leq 0.01$.

DISCUSSION

In this experiment, one-half of the goats were feed restricted between 90 d of pregnancy and parturition. During this experimental period, control goats maintained their BW, whereas restricted goats lost 8.2% BW. Moreover, the increase in plasma NEFA concentrations and the decrease in plasma glucose concentrations over the same period were greater in feed-restricted goats than in the control goats. These data show that the restriction of 70% compared with the energy eaten by ad libitum control goats was effective in inducing a loss in BW in the feed-restricted goats and inducing increased body reserve mobilization compared with control goats. On the basis of these results, we can conclude that the restricted goats were energy restricted and that the control goats were close to maintenance (no modification of BW, and only a slight decrease in glucose and a smaller increase in NEFA compared with the restricted goats). In addition, some feed-restricted goats became toxemic. Because kids of toxemic goats could not be studied and the health of the pregnant animals was compromised because of toxemia (Rook, 2000), the feed restriction was less severe at the end of gestation.

However, the treatment was effective because some morphometric and metabolic modifications were observed in kids. The birth weight of kids from triplet and twin litters was reduced in males born to feed-restricted goats. This reduction in birth weight has been already observed in male and female lambs (Koritnik et al., 1981; Oliver et al., 2001; Borwick et al., 2003; Husted et al., 2007) and in male and female goat kids in 1 study (Bajhau and Kennedy, 1990) but not in 2 others (Khan et al., 2005; Celi et al., 2008). In the present experiment, kid morphology was slightly influenced by maternal undernutrition during pregnancy but only at birth; the reduction in kid birth weight was associated with reduced abdominal girth and a trend for a reduction in BMI and density index. Oliver et al. (2001) found a reduction in birth weight associated with a reduction in crown-rump length and hock-to-toe length in lambs born to 20-d-restricted ewes in late pregnancy. Three months later, crown-rump length was shorter in males born to 20-d-restricted ewes. Thereafter, and until 1 yr after birth, no differences were found for any measurements. In the present experiment, no treatment effect was observed on male kid BW and morphometric measurements from 1 to 5 wk after birth. However, CONT male kids caught up their lighter birth weight during the first week after birth.

Several studies showed relationships between birth weight and pathologies. A very light birth weight has been shown to impair growth and metabolism in humans (Rosenberg, 2008), sheep (Greenwood et al., 1998), and pigs (Attig et al., 2008). Offspring with a very light birth weight are considered as intrauterine growth retarded animals (Anthony et al., 2003). However, in the work presented here, maternal feed restric-

Table 3. Suckling activity in the living pen during 24 h at 5 wk of age in male kids born to goats feed restricted during the last one-third of pregnancy (REST) or to control goats (CONT)[1,2]

Item	CONT (n = 13)	REST (n = 15)	SEM	*P*-value
Time spent with a teat in the mouth (i.e., suckling), min	29.5	27.7	5.68	0.76
Mean duration of a suckling bout,[3] s	0.044 (21.7)	0.038 (25.3)	3.28	0.39
Percentage of efficient suckling time[4]	38.1	40.9	6.05	0.18
Amount of milk, L/d	1.7	1.6	0.20	0.71

[1]The control goats were fed a total mixed ration (TMR) ad libitum for the last one-third of gestation and the feed-restricted goats were given the same TMR, but the quantity corresponded to 50 (for 4 wk), 60 (for 1 wk), 70 (for 1 wk), and 80% (for 2 wk) of the amount given to the control goats.

[2]Least squares means (back-transformed least squares means) and pooled SEM are presented.

[3]1/(x + 1) transformation.

[4]Time spent with a teat in the mouth and drinking.

tion reduced birth weight in the male offspring, but did not elicit growth retardation.

Body weight and litter size are related. Even if most of the studies in sheep mainly compared singles and twins (Edwards et al., 2005; Muhlhausler et al., 2008; Rumball et al., 2008), the same trend was always observed: the bigger the litter size, the lighter the offspring. These differences probably appeared in utero; NEFA concentration differences between the beginning and the end of feed restriction were greater in triplet-bearing goats than in twin-bearing goats. Moreover, BW loss during the feed restriction period was greater in triplet-bearing goats than in twin-bearing goats. Rumball et al. (2008) found decreased food intake and reduced glucose concentrations in late pregnancy in twin-bearing ewes compared with single-bearing ewes. In our experiment, after birth, growth variables (ADG, BMI, density index, and BW) were reduced in triplets compared with twins. Lighter kids remained smaller than heavier kids until 5 wk of age. Metabolism was also influenced by BW; glucose concentrations were greater in heavier kids at birth and at 1 and 3 wk of age, and insulin concentrations were greater in heavier

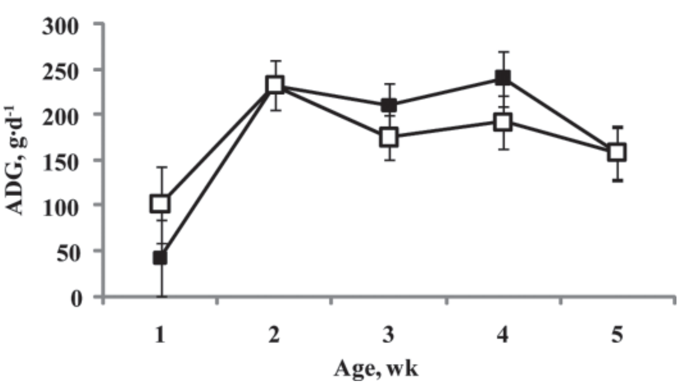

Figure 3. Average daily BW gain in male kids born to goats feed-restricted during the last one-third of gestation (□, n = 15) or to control dams (■, n = 13) from birth until 5 wk of age. The control goats were fed a total mixed ration (TMR) ad libitum for the last one-third of gestation, and the feed-restricted goats were given the same TMR, but the quantity corresponded to 50 (for 4 wk), 60 (for 1 wk), 70 (for 1 wk), and 80% (for 2 wk) of the amount given to the control goats. No differences were observed between groups.

kids at birth and 5 wk after birth. At slaughter, heavier kids had larger organs and heavier deposits of adipose tissue. Therefore, it seems that, as suggested by Mulhausler et al. (2008), BW rather than litter size per se may influence growth and body composition.

At birth, plasma NEFA concentrations were less in male and female REST kids compared with male and female CONT kids. In contrast to Celi et al. (2008), who found greater NEFA concentrations from birth to 5 wk of age in kids born to underfed goats, our results suggest that REST kids mobilized decreased adipose tissue reserves compared with CONT kids at birth. There were no further differences in NEFA concentrations thereafter between REST and CONT kids. Moreover, no treatment effect was observed on glucose, insulin, and leptin concentrations between birth and 5 wk of age However, in the work of Celi et al. (2008), kids were reared by their own dam and feed-restricted dams produced less milk, which can explain the discrepancies between the 2 studies.

In kids, feed intake is highly correlated to BW (Bas et al., 1985). A study in sheep showed that lambs born to feed-restricted dams were lighter and drank less milk replacer than control lambs (Geraseev et al., 2006). The authors hypothesized that lambs born to feed-restricted dams ate less because of a reduced digestive tract size. Differences in feeding behavior may not have been seen in our experiment because the differences in BW, and therefore in the digestive tract, were not large enough and disappeared rapidly after birth. Even if digestive tract size may be a limiting factor for feed intake, intake does not only depend on BW. Changes in feeding behavior and emotional reactivity were expected in the offspring after maternal nutritional restriction in late gestation. The maturation and activation of the hypothalamo-pituitary-adrenal axis occurs in late pregnancy in sheep (Matthews and Challis, 1996). The hypothalamus is an important regulator of feed intake (Della-Fera and Baile, 1984) and is involved in responses to stress (Hargreaves, 1990). Studies have shown in utero programming of thirst and feeding behavior in rats (Ross and Nijland, 1998; Langley-Evans et al., 2005) and of emotional reactivity in sheep (Erhard et al., 2004). However, 5 wk after birth, no modification in suckling behavior or emotional reactivity due to feed restriction during gestation was observed. This could be due to several reasons. First, undernutrition during the last third of pregnancy may not modify emotional and feeding behavior of goat kids. Studies in sheep and goats feed restricted in early pregnancy showed no modification in offspring reactivity up until 5 mo of age (Hernandez et al., 2009; Simitzis et al., 2009). Modifications in offspring born to late-pregnancy feed-restricted dams have never been investigated. The effects of undernutrition during gestation on the offspring may, however, only be observed in adults. Erhard et al. (2004) showed an increase in emotional reactivity in 18-mo-old lambs born to early-pregnancy underfed ewes. Moreover, in rodents, protein restriction during pregnancy or lactation modified intake behavior or both of the offspring after weaning and in adult life (Bellinger et al., 2004, 2006; Bellinger and Langley-Evans, 2005; Orozco-Sólis et al., 2009). In Ehrard et al. (2004), however, restriction was performed during early pregnancy. The effects on offspring emotional reactivity may not be the same depending on the timing of feed restriction, as already observed for metabolism and physiology. Maternal undernutrition in early pregnancy in humans and animal models leads to an increase in arterial blood pressure, whereas undernutrition in late pregnancy leads to insulin resistance and obesity problems (Symonds et al., 2009).

Second, the postnatal environment imposed in the present study may not favor maintenance of metabolic or behavioral differences between restricted and control kids. Suckling behavior in maternally fed lambs and kids is influenced by BW, age, breed, litter size, and dam experience, condition, and behavior (Ewbank, 1967; Festa-Bianchet, 1988; Dwyer et al., 1996, 2003). Feed restriction during pregnancy can affect maternal behavior (Terrazas et al., 2009) and milk production (Celi et al., 2008; Tygesen et al., 2008). Metabolic and behavioral modifications observed in kids or lambs reared by their mothers may, therefore, be due to impaired maternal behavior and milk production. Here, in artificially reared kids, the dam was not present. If some modifications were observed in kids born to restricted dams in this experiment, it would result directly from the maternal feed restriction during late pregnancy and not from impaired maternal behavior and milk production. There can be social facilitation that leads to a synchronization of behaviors in the rearing pens as shown for feeding and resting behavior in pigs (Nielsen et al., 1996), sheep (Rook and Penning, 1991), and cattle (Benham, 1982). Some authors also reported in pigs a desire to eat simultaneously with peers when the animal was observed in a social context (Hsia and Wood-Gush, 1984). Nielsen et al. (1996) showed that when groups of pigs had access to multi-space troughs, these pigs preferred feeding at the same time as, and adjacent to, other pigs that were eating. The synchronization of kid activities may have hidden, if it existed, the effect of maternal feed restriction.

In conclusion, maternal nutrition affected kid metabolism and morphology at birth, but these effects did not persist during the next 5 wk. In addition, kid emotional reactivity, as well as suckling behavior, at 3 and 5 wk of age was not affected by maternal feed restriction. Experiments carried out for longer periods to study the effects at adult age may reveal more effects of maternal feed restriction on offspring.

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