Domestic Animal Endocrinology 65 (2018) 24–37

Contents lists available at ScienceDirect

Domestic Animal Endocrinology

journal homepage: www.journals.elsevier.com/domestic-animal-endocrinology

Influence of postweaning feeding management of beef heifers on performance and physiological profiles through rearing and first lactation

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ARTICLE INFO

Article history:
Received 5 August 2017
Received in revised form 7 April 2018
Accepted 2 May 2018

Keywords:
Beef breeds
Lactation performance
Metabolic and hormone profiles
Pre-breeding feeding strategy
Replacement heifer growth

ABSTRACT

The aim of this study was to examine the effects of 2 postweaning feeding management approaches (FEED: 0.8 [HIGH] vs 0.6 [MOD] kg/d target ADG) on the performance of heifers of 2 beef breeds (BREED: Parda de Montaña [PA] vs Pirenaica) calving at 2 yr. Twenty-five heifers previously creep fed before weaning (6 mo) were assigned to 2 planes of nutrition from 6 to 15 mo of age. At 15 mo, they were inseminated, and then received similar diets until weaning of their first calf (4 mo postcalving). Several parameters were measured to analyze growth and development (BW; ADG; size measures at 6 mo, 15 mo, calving, and weaning), performance at puberty and first breeding, and dam and calf performance in the first lactation (calving traits, ADG, milk yield). Metabolic (glucose, cholesterol, NEFA, β-hydroxybutyrate, and urea) and endocrine status (IGF-I and leptin) were assessed in plasma samples collected every 3 mo from 6 mo to calving and monthly during lactation. No interaction between BREED and FEED was observed. Heifers from the HIGH feeding treatment had higher postweaning ADG than those on the LOW diet. At 15 mo, they had greater BW, heart girth, and external pelvic area, but they did not differ thereafter. All heifers reached puberty at similar BW (55% mature BW) but different ages. Heifers from the HIGH treatment tended ($P < 0.09$) to be pubertal earlier, and PA heifers were 1.6 mo younger than Pirenaica heifers ($P < 0.05$) at puberty. At the time of conception (452 ± 59 kg) and calving (471 ± 51 kg), BW was above common recommendations in all groups. Calving traits and performance in lactation did not differ between feeding treatments. BREED only influenced birth weight; PA calves being heavier ($P < 0.05$), which resulted in a larger calf/cow BW ratio, but no effect on calving difficulty or subsequent performance. Metabolic substrates and hormones depended mostly on sampling date, which was related to current energy and protein intake. Glucose ($P < 0.001$), cholesterol ($P < 0.001$), and IGF-I ($P < 0.05$) were greater during the postweaning phase in heifers on the HIGH diet, and persistent physiological effects were observed during lactation. Age at puberty was negatively related with IGF-I ($r = -0.43$, $P < 0.001$), but not with leptin concentrations. In conclusion, regardless of breed, a moderate growth rate ensured adequate heifer development and performance until the first lactation, whereas no advantage was gained from enhanced postweaning gains.

1. Introduction

To decrease the cost of rearing beef heifers, it is recommended to advance the first calving to 2 yr, for which they should be bred at 15 mo and be pubertal at least

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https://doi.org/10.1016/j.domaniend.2018.05.001

6 wk before [1]. Age at puberty depends on the diets applied from 4 to 6 mo [2] and after weaning [3]. To achieve this target, postweaning growth should guarantee that heifers reach 65% of mature BW at breeding [4], although other studies proposed to reduce this threshold to 50%–55% [5,6]. Moreover, the heifers should reach 80% of mature BW [7] at first calving, with adequate skeletal development. Recently, Rodríguez-Sánchez et al [8] indicated that beef heifers calving at 2 yr should gain at least 1 kg/d either before or after weaning to prevent impaired performance at calving. In mountain areas, where cow-calf pairs are housed and calves are creep fed [9], it is safer to ensure this gain before than after weaning, when heifers are turned out to pasture.

The effects of accelerated gains of dairy heifers on adult performance have been given wide attention in the literature [10], but optimal growth rates for beef cattle have yet to be defined. Overnutrition during heifer development has been associated with decreased milk production [11] because it hastens puberty and reduces the duration of the first allometric phase of development of the mammary gland [12]. This effect has been widely studied in dairy cows [13], but it is also of major interest in beef cows because milk yield is one of the main factors that determine calf weaning weight.

Feeding after weaning affects the metabolic and endocrine profiles, and consequently development and reproductive performance [14]. This long-term effect of nutritional interventions in the young calf on physiological outcomes later in life is known as metabolic imprinting [15]. Moreover, because breeds can differ in growth patterns and age at puberty, management should be tailored to avoid underfeeding or overfeeding [16].

Parda de Montaña (PA) and Pirenaica (PI) are 2 beef breeds widely spread in the mountain areas of Spanish Pyrenees. The first comes from the old Brown Swiss selected for beef production, whereas the second is an autochthonous hardy breed used for beef production. Although their mature BW is similar [17], other production traits differ. Parda de Montaña calves are heavier at birth and, due to the greater cow milk yield [18], when not supplemented, they are heavier at weaning than PI calves [19]. Thereafter, PA is an intermediate-maturing breed and PI a late-maturing one [20].

We hypothesized that accelerated gains from weaning to breeding would improve the performance of beef heifers at first breeding and in their first lactation. Our second hypothesis was that both breeds could be raised under the same heifer feeding program designed to ensure a timely match of their requirements.

This study aimed to assess the effects of 2 feeding managements after weaning designed to promote different gains (0.8 vs 0.6 kg/d) from 6 to 15 mo of age in 2 breeds of beef heifers (PA vs PI) on performance, until weaning of their first calf. Heifer development, performance and metabolic (glucose, cholesterol, NEFA, β-hydroxybutyrate, urea) and endocrine status (IGF-I and leptin) were analyzed through their rearing phase, pregnancy, and lactation.

2. Materials and methods

The Animal Ethics Committee of the Centro de Investigación y Tecnología Agroalimentaria (CITA) approved the experimental procedures, which were in compliance with the guidelines of the European Union [21] on the protection of animals used for experimental and other scientific purposes.

2.1. Animals, management, and diets

This study was conducted at CITA–Montañana Research Station (postweaning phase, 41°43′ N, 0°48′ W, 225 m above sea level, mean annual temperature 15.2 ± 0.2°C, and mean annual rainfall 318 ± 63 mm) and CITA–La Garcipollera Research Station, in the mountain area of central Pyrenees (gestation and lactation, 42°37′ N, 0°30′ W, 945 m above sea level, mean annual temperature 10.2 ± 0.2°C, and mean annual rainfall 1,059 ± 68 mm).

Twenty-five 6-mo-old heifers, born from an autumn-calving herd (October 11 ± 10 d) of 65 adult cows of PA and PI breeds, were distributed in a 2 by 2 factorial arrangement: 2 breeds (BREED: PA vs PI) by 2 feeding treatments to promote different growth rates (FEED: 0.8 kg/d [HIGH] and 0.6 kg/d [MOD] treatments, respectively) during the postweaning phase (from weaning at 6 mo to breeding at 15 mo). This resulted in 4 experimental groups: PA-HIGH (7 heifers), PA-MOD (6), PI-HIGH (6), and PI-MOD (6) (Fig. 1). The experiment started when the calves

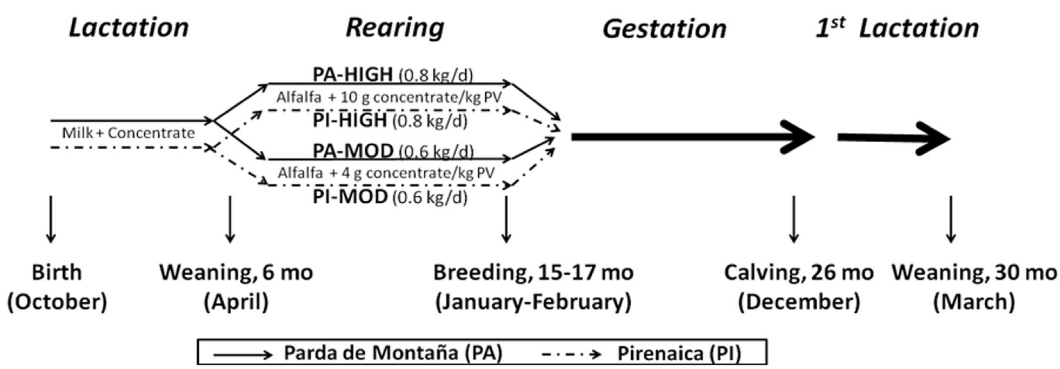

Fig. 1. Experimental design with the postweaning diets and the target ADG for each breed (BREED) and feeding management (FEED).

were weaned at 6.4 ± 0.3 mo and 238 ± 41 kg BW. Treatments were randomly balanced according to calf BW and age. During the previous lactation phase, they were fed on their dam's milk (suckling twice daily for 30 min) and had free access to a starter concentrate (Table 1), resulting in preweaning gains of 1.04 ± 0.18 kg/d.

During the postweaning phase, heifers were maintained indoors in a loose housing system in straw-bedded pens. All pens assigned to heifers of each experimental group in this phase were in the same barn, similar in size and environmental conditions. Fresh and clean water and vitamin-mineral supplements (lick blocks) were supplied ad libitum. To achieve the targeted weight gains, heifers were group fed alfalfa hay ad libitum and 10 g (HIGH) or 4 g concentrate/kg BW (MOD) (44% corn, 22% barley, 15% corn gluten, 5% rapeseed flour, 5% soybean flour, 3% beet pulp, 3% palm oil, 3% vitamin-mineral supplements; Table 1). Concentrate was provided daily at 08:00 h, and heifers were tied up for a maximum of 1 h until they finished the restricted amount assigned to each one. Alfalfa hay was provided ad libitum in metal feeding troughs, refilled twice daily and long enough for all heifers in the pen to eat at the same time and avoid competition.

When heifers reached 15 mo of age, a 60-d breeding season began, during which they were managed as a single group. In this phase they were fed 9 kg/head/d of a dry total mixed ration (46% barley straw, 12% alfalfa hay, 18% barley, 8% sugarcane molasses, 6% soybean meal, 4% cereal by-products, 4% rapeseed, 2% sunflower seed; Table 1). All heifers were synchronized with an Ovsynch + progesterone-releasing intravaginal device (PRID) program, in which they simultaneously received 1.55 mg of progesterone in a PRID (CEVA, Barcelona, Spain) and a 10 μg injection of GnRH (Busol; INVESA, Barcelona, Spain) followed 10 d later by 25 mg of prostaglandin $F_{2\alpha}$ (Enzaprost; CEVA). The PRID was removed 12 d later, and 500 IU of pregnant mare serum gonadotrophin (Folligon; Intervet, Salamanca, Spain) were administered followed 48 h later by a second injection of GnRH (10 μg). Eight hours after the final GnRH injection, heifers were inseminated by an expert technician. Three different sires for each breed were selected for their calving ease, and semen from each of the 3 bulls was equally distributed in the feeding treatments per breed.

Heifers were checked twice daily (07:00 and 19:00 h) from the first AI to the end of the breeding season for detecting estrus of nonpregnant heifers. They were inseminated approximately 12 h after estrus detection. Return to estrus after each AI was considered as a diagnostic indicator of nonpregnancy status. Pregnancy was confirmed by ultrasonography (Aloka SSD-500V; equipped with a linear-array 7.5 MHz transducer; Aloka, Madrid, Spain) 31 d after the end of the breeding season.

The day of the first timed AI was used to determine age and BW at first breeding. First-service fertility rate was determined as number of pregnant heifers at the first AI divided by total number of heifers, and overall fertility rate was determined as the number of pregnant heifers in the breeding season divided by the total number of heifers.

Two heifers failed to get pregnant and were removed from the experiment at the end of the breeding season, which resulted in the following composition of the experimental groups thereafter: PA-HIGH (6 heifers), PA-MOD (6), PI-HIGH (6), and PI-MOD (5).

From the confirmation of pregnancy until a month before the expected calving date for each heifer, they grazed on mountain meadows (4 heifers/hectare) following the traditional management system [17]. These pastures were composed primarily of grasses (*Festuca arundinacea, Festuca pratensis,* and *Dactylis glomerata*), legumes (*Trifolium repens*), and other species (1,191 kg dry matter/ha, Table 1). In the last month of gestation, heifers were housed and fed 9 kg/animal/d of meadow hay (Table 1).

After calving, primiparous cows reared their calves for 4 mo. During their first lactation, dams received 10 kg/animal/d of the same dry total mixed ration provided during the breeding season. The diet was calculated to meet the requirements for energy and protein of maintenance, growth, and milk production of a cow of 490 kg BW and 6 kg daily milk yield. Calves of primiparous cows had free access to suckle their dams and received no other feed during the lactation period. All pens assigned to animals of each feeding treatment for each phase throughout the experiment were in the same barn, similar in size and environmental conditions. Water and vitamin-mineral supplements (lick blocks) were supplied for ad libitum intake throughout the experiment.

2.2. Measurements and blood sampling

During the postweaning phase, concentrate intake was recorded daily by group and monthly adjusted by average group weight. Intake of alfalfa hay was recorded by pen at weekly intervals. Actual daily intake in the indoor phases was calculated as feed provided minus feed refused, and during the grazing season it was estimated on a monthly

Table 1
Nutrient composition of the feedstuffs provided in the different phases.

Item	Starter concentrate[a]	Rearing concentrate[b]	Alfalfa hay[b]	Total mixed ration[c]	Grazed pasture [d]	Meadow hay[e]
DM, g/kg	894	900	851	897	242	883
ME, MJ/kg DM	15.1	15.2	9.2	9.6	10.5	11.3
CP, g/kg DM	166	147	98	103	197	84
NDF, g/kg DM	214	252	462	595	553	646

[a] Preweaning phase.
[b] Postweaning phase.
[c] Breeding season (60 d) and lactation (120 d).
[d] Gestation (from confirmation of pregnancy until a month before the expected calving date).
[e] Last month of gestation.

basis considering that pasture intake had met the requirements of the heifers according to their BW, ADG, and month of gestation.

Feed samples were collected at weekly intervals and were pooled on a monthly basis for chemical analyses. Samples were dried at 60°C until constant weight and mill-ground (1 mm screen), and dry matter, ash, ether extract, and CP (N × 6.25) contents were determined according to the Association of Official Analytical Chemists [22] (methods 942.05, 920.39, 968.06). Analyses of neutral detergent fiber, acid detergent fiber, and acid detergent lignin were conducted according to the sequential procedure of van Soest et al [23]. All values were corrected for ash-free content.

Heifers were weighed once a week before morning feeding, without prior deprivation of feed and water. Weight at keypoints (6, 9, 12, 15 mo, puberty onset, first breeding, calving, and weaning) was calculated as the average of 3 consecutive weights. Daily weight gains (postweaning, weaning to puberty, gestation, and lactation phases) were calculated by linear regression of weight against time. Calves were weighed at calving and thereafter weekly until weaning at 4 mo of age to determine their ADG during lactation. At 15 mo, calving and weaning, BCS was assessed by 2 expert technicians on a 0 to 5 scale, based on the estimation of fat covering loin, ribs, and tailhead.

Body development was studied using size measurements at 6 and 15 mo, calving and weaning. Height at withers (from the highest point of the shoulder blade to the ground), rump width (maximum distance between iliac tuberosities), and rump length (from the ischial tuberosity to the iliac tuberosity) were recorded with a height stick. External pelvic area was estimated as the product of rump width and rump length. Heart girth (body circumference immediately posterior to front legs) was measured with a flexible tape.

Calving ease was classified into 2 categories, that is, assisted or unassisted. Assisted calving included all types of assistance, from manual pull to a cesarean section as described by Johanson and Berger [24]. Ratio of calf/cow BW was estimated to determine fetal-maternal disproportion, as calf birth weight divided by cow weight at calving expressed as a percentage [24].

Primiparous dams were milked monthly during the 4 mo of lactation, using the oxytocin and machine milking technique 6 h after calf removal [25], to determine quantity and composition of the milk produced daily. Milk fat and protein contents were analyzed with an infrared scan (Milkoscan 4000; Foss Electric Ltd, Hillerod, Denmark). Energy-corrected milk (ECM) yield (adjusted to 3.5% fat and 3.2% protein) was calculated as described in Casasús et al [26].

Blood samples were collected weekly to determine the onset of puberty based on plasma progesterone concentration. In addition, blood samples were collected every 3 mo during the postweaning phase and gestation and monthly during lactation to determine concentrations of both metabolites and hormones. Blood samples were collected before morning feeding from the coccygeal vein. Samples to determine progesterone, ß-hydroxybutyrate, IGF-I, and leptin concentrations were collected into 9 mL heparinized tubes (Vacuette España S.A., Madrid, Spain). Samples to determine plasma glucose, cholesterol, NEFA, and urea concentrations were collected into 9 mL tubes containing EDTA (Vacuette España S.A.). Blood samples were centrifuged at 1,500 × g for 20 min at 4°C immediately after collection, and the plasma was harvested and frozen at −20°C until analysis.

All measurements and samples taken at 6 mo were conducted before postweaning diets were applied.

2.3. Assays

The concentrations of progesterone in plasma samples were measured using an ELISA kit specific for cattle (Ridgeway Science, Lydney, UK), following the manufacturer's instructions. The onset of puberty was considered to occur when progesterone levels were ≥1.0 ng/mL in at least 2 consecutive samples (normal estrus cycle, ≥ 14 d; [27]). Age at puberty was defined as date of collection of the first blood sample that contained ≥1.0 ng/mL of plasma progesterone. To ensure the continuation of estrous cycles, blood samples analyzed after the attainment of puberty were confirmed by observation of at least 1 subsequent estrous cycle of normal duration, based on progesterone concentration.

Plasma concentrations of glucose (glucose oxidase/peroxidase method), cholesterol (enzymatic-colorimetric method), ß-hydroxybutyrate (enzymatic-colorimetric method), and urea (kinetic UV test) were determined with an automatic analyzer (GernonStar, RAL/TRANSASIA, Dabhel, India). Protocols and reagents for glucose, cholesterol, and urea analyses were provided by the analyzer manufacturer (RAL, Barcelona, Spain), and reagents for ß-hydroxybutyrate were supplied by Randox Laboratories Ltd (Crumlin Co, Antrim, UK). Samples were run in duplicate.

Mean intra- and inter-assay CV for these metabolites were <5.4% and <5.8%, respectively. Sensitivity was 0.056, 0.026, 0.030, and 0.170 mmol/L for glucose, cholesterol, ß-hydroxybutyrate and urea, respectively. Plasma concentrations of NEFA were analyzed with an enzymatic method using a commercial kit (Randox Laboratories Ltd). Commercial reference plasma samples (bovine precision serum; Randox Laboratories Ltd) were used to evaluate the accuracy of the analyses. Mean intra- and inter-assay CV were 5.1% and 7.4%, respectively. Sensitivity was 0.060 mmol/L.

Circulating IGF-I concentrations were quantified with a solid-phase enzyme-labeled chemiluminescent immunometric assay (IMMULITE; Siemens Medical Solutions Diagnostics Limited, Llanberis, Gwynedd, UK). Mean intra- and inter-assay CV were 3.1% and 12.0%, respectively. Sensitivity was 20 ng/mL.

Plasma leptin concentrations were determined by RIA with a multispecies commercial kit (Multispecies Leptin RIA kit; LINCO Research, St. Charles, MO). Mean intra- and inter-assay CV were 3.54% and 6.87%, respectively. Sensitivity averaged 1.30 ng/mL.

2.4. Statistical analyses

All data were analyzed as a completely randomized design with the SAS statistical software package (SAS Institute Inc, Cary, NC). Heifer was considered the experimental unit. Data for BW, ADG, BCS, size measures (height

Table 2
Weights, ADG, and BCS of heifers throughout the study according to breed (BREED) and feeding management (FEED) applied in the postweaning period (6 to 15 mo).

Item	BREED		FEED		SEM	*P*-value	
	PA[e]	PI[e]	HIGH[e]	MOD[e]		BREED	FEED
n[f]	13 (12)	12 (11)	13 (11)	12 (12)			
Weight, kg							
6 mo	247	229	235	241	17.6	0.30	0.76
15 mo	441	410	452[c]	400[d]	21.3	0.15	0.02
Calving	477	464	480	461	21.9	0.58	0.43
Weaning	479	475	489	465	20.2	0.84	0.28
ADG, kg/d							
Postweaning	0.737	0.700	0.814[c]	0.624[d]	0.0342	0.27	<0.001
Gestation	0.040	0.102	0.030	0.111	0.0408	0.58	0.32
Lactation	0.017	0.083	0.071	0.030	0.0730	0.39	0.59
BCS (0–5)							
15 mo	4.1	4.2	4.3	3.9	0.22	0.76	0.06
Calving	2.7	2.8	2.8	2.7	0.11	0.60	0.56
Weaning	2.6[b]	2.8[a]	2.8	2.7	0.06	0.008	0.34

[a,b]LSMeans within a row with different superscripts differ significantly among breeds ($P < 0.05$).
[c,d]LSMeans within a row with different superscripts differ significantly between feeding managements ($P < 0.05$).
[e] PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.
[f] n, heifers per treatment in the postweaning phase (heifers per treatment during gestation and lactation).

at withers, heart girth, and external pelvic area), ECM yield and milk quality, metabolic (glucose, cholesterol, NEFA, ß-hydroxybutyrate, and urea) and endocrine (IGF-I and leptin) profiles were analyzed using the SAS MIXED procedure for repeated measures. Covariance structure was selected on the basis of the lowest Akaike information criterion. Therefore, an unstructured covariance matrix was used for analysis of repeated measures, which included BREED, FEED, sampling date, and their interaction as fixed effects and with heifer as the random effect in a univariate linear mixed model.

Age and weight at puberty and at the first AI were tested with ANOVA using the GLM procedure, where BREED, FEED, and their interaction were fixed effects. Fertility rate at first AI and at the end of the breeding period were analyzed using the GLIMMIX procedure, considering BREED and FEED as fixed effects and AI sire as the random effect, with a logit link and a binomial distribution.

Calf performance (BW at birth and weaning, and ADG) and calf/cow BW ratio were tested with ANOVA using the GLM procedure, with the fixed effects of BREED, FEED, sire used for AI, calf sex, and their interaction. Calf sex effect was analyzed using the FREQ procedure (χ^2 test). Calving assistance was analyzed using the GLIMMIX procedure, considering BREED, FEED, and calf sex as fixed effects and AI sire as the random effect, with a logit link and a binomial distribution. The model also analyzed the effects of the length of gestation, calving date, and calf/cow BW ratio.

Pearson correlation coefficients between all variables at a given time point, and between all time points for a given metabolite or hormone, were calculated using the CORR procedure. Where not stated, correlations were not significant. Means were separated using the LSMeans procedure. For all tests, level of significance was $P < 0.05$, and tendencies were determined if $P \geq 0.05$ and $P < 0.10$.

Total energy and protein intake were not tested statistically as the data recorded to calculate them were registered on a group basis, and hence, only absolute data are presented.

3. Results

3.1. Growth performance

The interaction between BREED and FEED was not significant ($P > 0.10$) at any date and for any growth trait

Table 3
Size measures of heifers throughout the study according to breed (BREED) and feeding management (FEED) applied in the postweaning period (6 to 15 mo).

Item	BREED		FEED		SEM	*P*-value	
	PA[e]	PI[e]	HIGH[e]	MOD[e]		BREED	FEED
n[f]	13 (12)	12 (11)	13 (11)	12 (12)			
Height at withers, cm							
6 mo	100.9	100.3	100.8	100.4	2.24	0.81	0.87
15 mo	121.0	120.1	122.4	118.8	2.08	0.65	0.09
Calving	128.1	127.4	128.6	126.9	1.84	0.73	0.37
Weaning	128.1	128.0	128.1	128.0	1.85	0.97	0.99
Heart girth, cm							
6 mo	136.0	132.9	133.7	135.2	3.62	0.40	0.69
15 mo	178.5	173.5	181.2[c]	170.8[d]	2.99	0.10	0.002
Calving	177.1	176.1	178.4	174.8	2.72	0.73	0.22
Weaning	177.1	175.8	178.1	174.8	2.56	0.64	0.23
External pelvic area, dm^2							
6 mo	11.4	10.1	10.6	10.9	0.67	0.05	0.62
15 mo	21.7[a]	19.0[b]	21.4[c]	19.3[d]	0.93	0.009	0.04
Calving	24.5	24.0	24.5	24.5	1.05	0.63	0.75
Weaning	25.3	24.6	25.1	25.1	1.03	0.47	0.76

[a,b]LSMeans at a given age with different superscripts differ significantly between breeds ($P < 0.05$).
[c,d]LSMeans at a given age with different superscripts differ significantly between feeding managements ($P < 0.05$).
[e] PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.
[f] n, heifers per treatment in the postweaning phase (heifers per treatment during gestation and lactation).

Table 4
Reproductive performance of heifers at breeding according to breed (BREED) and feeding management (FEED) applied in the postweaning period (6 to 15 mo).

Item	BREED		FEED		SEM	*P*-value	
	PA[e]	PI[e]	HIGH[e]	MOD[e]		BREED	FEED
n	13	12	13	12			
Weight at puberty, kg	321	325	321	326	15.68	0.81	0.75
Age at puberty, mo	9.1[b]	10.7[a]	9.4	10.5	0.62	0.01	0.09
ADG 6 mo-puberty	0.997	0.827	1.067[c]	0.757[d]	0.0894	0.07	0.002
% MBW[f] at puberty	55.4	56.0	56.1	55.3	0.03	0.81	0.75
Weight at first AI, kg	458	423	467[c]	414[d]	22.08	0.12	0.02
Age at first AI, mo	15.7	15.8	15.8	15.8	0.14	0.55	0.99
Fertility at first AI, %	31	50	31	50		0.32	0.33
Fertility[g], %	92	92	85	100		0.91	0.18

[a,b]LSMeans at a given age with different superscripts differ significantly between breeds ($P < 0.05$).
[c,d]LSMeans at a given age with different superscripts differ significantly between feeding managements ($P < 0.05$).
[e] PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.
[f] MBW, mature BW.
[g] Fertility rate in a 60-d breeding season.

assessed; therefore, the main effects are presented separately.

Heifer weight at keypoints, ADG, and BCS during the postweaning phase, gestation, and lactation are displayed in Table 2. At the start of the study, BW did not differ between breeds, and because ADG were similar thereafter, they had similar weight at 15 mo, calving, and weaning. The BCS at 15 mo and calving were also similar between breeds, but during lactation, PA cows showed a slight loss of BCS, whereas PI primiparous maintained it; therefore, BCS at weaning was greater in PI than in PA cows ($P < 0.01$).

Gains during the postweaning phase differed between both FEED treatments ($P < 0.001$). Consequently heifers from the HIGH treatment were heavier than those from the MOD treatment at 15 mo ($P < 0.05$), and BCS also tended to be greater ($P = 0.06$). This difference was compensated for during gestation, and thereafter, weight and BCS at calving and weaning did not differ between feeding strategies, and neither did ADG during lactation.

Size measurements are shown in Table 3. Heifers of both breeds had similar height at withers and heart girth throughout the experiment, both being strongly and positively correlated with BW (r = 0.88 and 0.90, respectively, $P < 0.001$). The external pelvic area tended to be greater in PA heifers at 6 mo ($P = 0.05$) and was significantly greater at 15 mo ($P < 0.01$), but it did not differ at calving. This trait was also correlated with BW (r = 0.90, $P < 0.001$).

No differences were observed between feeding strategies at 6 mo, but at 15 mo, height at withers tended to be greater in heifers from the HIGH feeding treatment ($P = 0.09$), and they had greater heart girth ($P < 0.01$), which corresponded with their greater BW at this point. They also had a larger external pelvic area ($P < 0.05$) at this point, but throughout gestation all these differences were offset and values were similar at calving and at weaning.

3.2. Productive performance

Heifer performance at puberty and first breeding was not influenced by the interaction between BREED and FEED, and therefore, results of the main effects are presented in Table 4. All heifers were pubertal before the breeding season, reaching puberty at similar BW (322 ± 38 kg), which was 55.5% of expected mature BW (580 kg for both breeds; [17]).

Age at puberty was different between breeds, with PA heifers attaining puberty earlier than PI heifers ($P < 0.05$). Heifers from the HIGH feeding treatment tended to be pubertal 1 mo earlier ($P = 0.09$) than those from the MOD treatment. Consistent with this trend, a strong negative correlation between age at puberty and weaning-to-puberty

Table 5
Performance of primiparous dams in the first calving and lactation according to breed (BREED) and feeding management (FEED) applied in the postweaning period (6 to 15 mo).

Item	BREED		FEED		SEM	*P*-value	
	PA[c]	PI[c]	HIGH[c]	MOD[c]		BREED	FEED
n	12	11	11	12			
Cow							
Age at first calving, mo	26.0	25.8	25.8	26.1	0.39	0.61	0.39
Calving assistance, %	58	10	18	55		0.13	0.13
Calf/Cow BW ratio, %	8.1[a]	7.1[b]	7.4	7.1	0.42	0.04	0.42
Calf							
Male/female ratio	8/4	5/6	6/5	6/6		0.21	0.99
Birth BW, kg	38.0[a]	33.0[b]	35.4	35.6	1.68	0.01	0.90
Weaning BW, kg	119.0	114.5	118.7	113.8	5.28	0.36	0.41
ADG, kg	0.675	0.675	0.694	0.655	0.041	0.99	0.39

[a,b]LSMeans within a row with different superscripts differ significantly between breeds ($P < 0.05$).
[c] PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.

Table 6
Milking performance in the first lactation of heifers according to breed (BREED) and feeding management (FEED) applied in the postweaning period (6 to 15 mo).

Item	BREED				SEM	*P*-value		
	PA[c]		PI[c]					
	FEED					BREED	FEED	BREED × FEED
	HIGH[c]	MOD[c]	HIGH[c]	MOD[c]				
n	6	6	6	5				
Yield, kg/d	5.51[a]	4.60[b]	4.36[b]	5.86[a]	0.58	0.84	0.33	<0.001
Protein content, %	3.44[ab]	3.34[b]	3.62[a]	3.42[b]	0.12	0.049	0.02	0.45
Fat content, %	3.56[b]	3.42[b]	4.51[a]	4.11[a]	0.35	<0.001	0.15	0.50

[a,b]LSMeans within a row with different superscripts differ significantly among experimental groups ($P < 0.05$).
[c] PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.

ADG of heifers (r = −0.70, $P < 0.001$) was observed. All heifers were pubertal at least 2 mo before the first AI, except for 1 PI–MOD heifer who was pubertal only 1 mo before.

As shown in Table 4, BW at the first AI did not differ between breeds, despite PI heifers being 35 kg lighter, most likely because of the low BW reached by PI–MOD heifers (389 ± 51 kg). As expected, BW at the first AI was affected by FEED ($P < 0.05$) with heifers from the HIGH feeding treatment being 53 kg heavier. Despite this difference, BW in all experimental groups was greater than 65% of the expected mature BW (381 kg). Fertility rate at the first AI and at the end of the breeding season were similar among treatments, and were not influenced by AI sire.

Dam and calf traits in the first lactation are presented in Table 5 according to BREED and FEED, because they were not affected by an interaction between these main effects. Age at first calving was similar in all treatments (25.9 ± 0.9 mo). Assistance at calving was needed in 36% of the primiparous cows, and mostly consisted of the use of a calving jack, cesarean section not being needed in any case. The disproportion between cow and calf BW, that is, the calf/cow BW ratio, was greater in PA than in PI cows (8.1% vs 7.1% respectively, $P < 0.05$). However, differences among treatments in incidence of calving assistance related to BREED, FEED, sire used for AI, gestation length, calving date, calf sex, or calf/cow BW ratio were not significant ($P > 0.10$).

The calf sex ratio was similar among treatments ($P > 0.10$), and no differences were observed between sexes in calf weight at birth (36.7 vs 33.2 kg BW in male and female calves, respectively, SEM = 2.33, $P > 0.10$) or at weaning (112.2 vs 117.9 kg BW, SEM = 7.31, $P > 0.10$), nor in the calf ADG during lactation (0.629 vs 0.710 kg ADG, SEM = 0.083, $P > 0.10$), and neither among sires (data not shown). No other dam productive or reproductive trait analyzed herein was influenced by calf sex. As shown in Table 5, PA calves were 5 kg heavier at birth than PI calves ($P < 0.01$). Thereafter, calf performance was unaffected by BREED or FEED treatments, showing similar gains during the 120 d of lactation (0.669 ± 0.104 kg/d), which resulted in a similar weight at weaning (116.1 ± 12.9 kg).

The average milk yield of primiparous cows during lactation (Table 6) was affected by the interaction between BREED and FEED ($P < 0.001$), and so was the ECM, which was stable during the first 2 mo of lactation and decreased in the last month (Fig. 2). The overall milk production was unexpectedly low (5.05 vs 5.11 kg/d in PA and PI respectively, $P > 0.10$), especially in PA cows. Milk fat and protein contents were lower in PA than in PI cows (3.49% vs 4.31% fat, respectively, $P < 0.001$; 3.39% vs 3.52% protein, respectively, $P < 0.05$). Finally, a FEED effect on the milk protein was observed, this content being greater in HIGH than in MOD treatments (3.53% vs 3.38%, respectively, $P < 0.05$).

3.3. Metabolic profiles

Estimated energy and protein intake depending on the breed and feeding management are presented in Figure 3. The profiles of different metabolites are shown in Figure 4 according to BREED and FEED, because there was no interaction between both effects, but all of them were affected by sampling date ($P < 0.001$). For all metabolites, the correlations between concentrations observed at 6 mo, 15 mo, calving, and weaning were not significant ($P < 0.10$).

The greatest concentrations of glucose were observed at 6 mo (6.25 ± 0.10 mmol/L), and thereafter, they decreased throughout gestation to a nadir observed 1 wk before calving (3.49 ± 0.06 mmol/L). Glucose concentrations did not differ between breeds ($P > 0.10$). Mean values were greater in heifers from HIGH feeding management than in

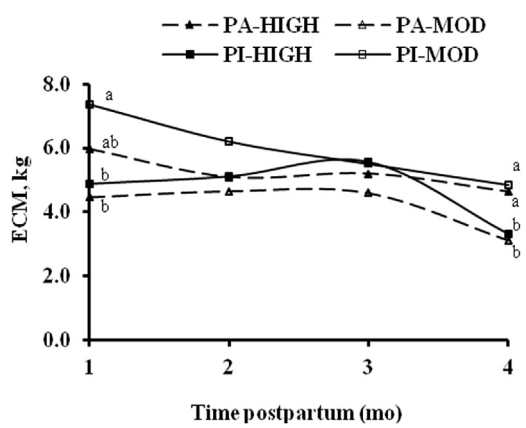

Fig. 2. Energy-corrected milk (ECM) yield throughout the first lactation of beef heifers according to breed and feeding management applied in the postweaning period (6 to 15 mo). [a,b]LSMeans at a given month with different superscripts differ significantly among treatments ($P < 0.05$). PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.

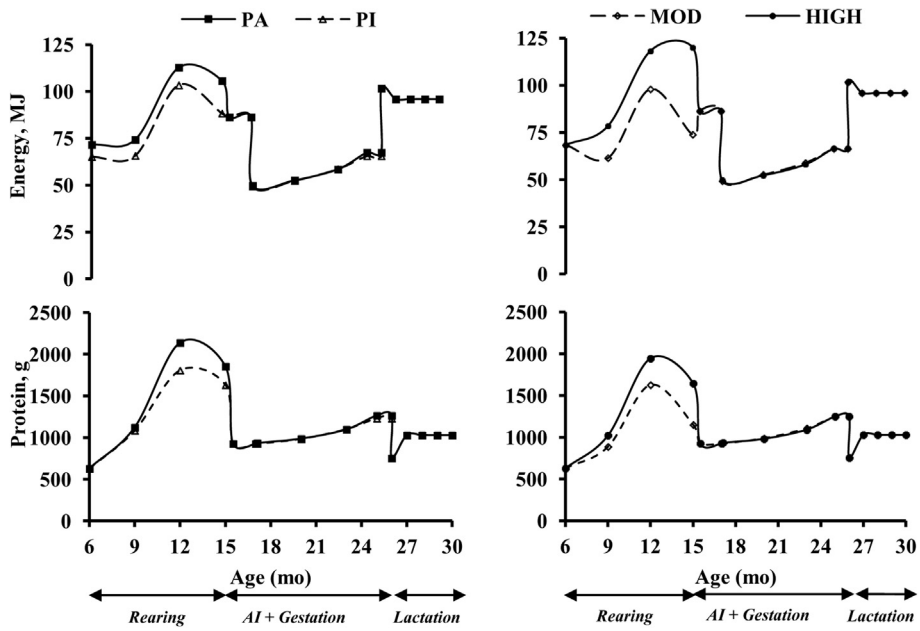

Fig. 3. Estimated energy and protein intake by heifers during the experiment according to breed and feeding management applied in the postweaning period (6 to 15 mo). PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.

the MOD group (4.37 vs 4.18 mmol/L, respectively, $P < 0.001$). Glucose was positively correlated with ADG and BCS ($r = 0.79$ and 0.69, respectively, $P < 0.001$) throughout the study.

Regarding cholesterol, the greatest values were also observed at 6 mo (4.50 ± 0.14 mmol/L) and its nadir was found before calving (2.43 ± 0.10 mmol/L). Plasma cholesterol values were lower in PA than in PI heifers (2.91 vs 3.23 mmol/L, respectively, $P < 0.05$). Besides, an interaction was observed between sampling date and FEED ($P < 0.001$). During the postweaning phase, cholesterol values were greater in the HIGH feeding management group, but they did not differ during gestation, and during lactation, the highest values were observed in dams from the MOD treatment. Moreover, cholesterol and glucose levels were strongly correlated ($r = 0.51$, $P < 0.001$). During lactation, cholesterol concentration was positively associated with milk yield of dams ($r = 0.38$, $P < 0.001$).

Plasma NEFA concentrations were affected by BREED (0.20 vs 0.24 mmol/L in PA and PI, respectively, $P < 0.05$), but not by FEED. They increased as gestation progressed to the greatest values observed at calving (0.45 ± 0.08 mmol/L). They then showed a marked drop during lactation to a nadir at weaning (0.04 ± 0.01 mmol/L), being correlated with cow milk yield in the first month of lactation ($r = 0.55$, $P < 0.01$).

Concerning ß-hydroxybutyrate, the influence of FEED depended on sampling date ($P < 0.001$), with greater values in the HIGH feeding treatment only during the postweaning period. In this phase, the concentrations of ß-hydroxybutyrate and NEFA were negatively correlated ($r = -0.51$, $P < 0.01$). Thereafter, they did not differ across BREED or FEED with advancing gestation and lactation.

Plasma urea concentration increased throughout the postweaning phase to its greatest value at 15 mo (6.5 ± 0.14 mmol/L), decreased during pregnancy to a nadir at the start of lactation (3.8 ± 0.16 mmol/L) and increased again thereafter, regardless of BREED or FEED. Urea concentration at 6 mo was positively related to cholesterol concentration ($r = 0.47$, $P < 0.05$) and negatively to age at puberty of heifers ($r = -0.58$, $P < 0.01$).

3.4. Endocrine profiles

Profiles of plasma IGF-I and leptin are presented in Figure 5 according to BREED and FEED. The concentration of both hormones was affected by sampling date ($P < 0.001$).

The greatest level of IGF-I was observed at the start of study (283 ± 13.1 ng/mL), and individual values were associated with preweaning weight gains ($r = 0.40$, $P < 0.01$). Thereafter, levels of IGF-I remained steady during the postweaning period, decreased through gestation to a nadir at calving (53 ± 6.9 ng/mL), and then increased as lactation progressed. Values for IGF-I did not differ between breeds but they were affected by FEED, with greater values observed in the HIGH than in the MOD feeding treatment (145 vs 120 ng/mL, respectively, $P < 0.05$). Heifers with higher concentrations of IGF-I had greater weight gains ($r = 0.83$) and BCS ($r = 0.74$) throughout the experiment and attained puberty earlier ($r = 0.43$) ($P < 0.001$ in all cases). Positive relationships were also found between IGF-I and glucose ($r = 0.66$), cholesterol ($r = 0.29$), and urea ($r = 0.30$) levels during the trial, and a negative relation with concentrations of NEFA ($r = -0.21$) ($P < 0.001$). At the individual level, IGF-I concentrations were related across sampling times because correlations were observed between samples obtained at 6 and 15 mo ($r = 0.54$, $P < 0.001$) and up to weaning of the first calf ($r = 0.63$, $P < 0.01$).

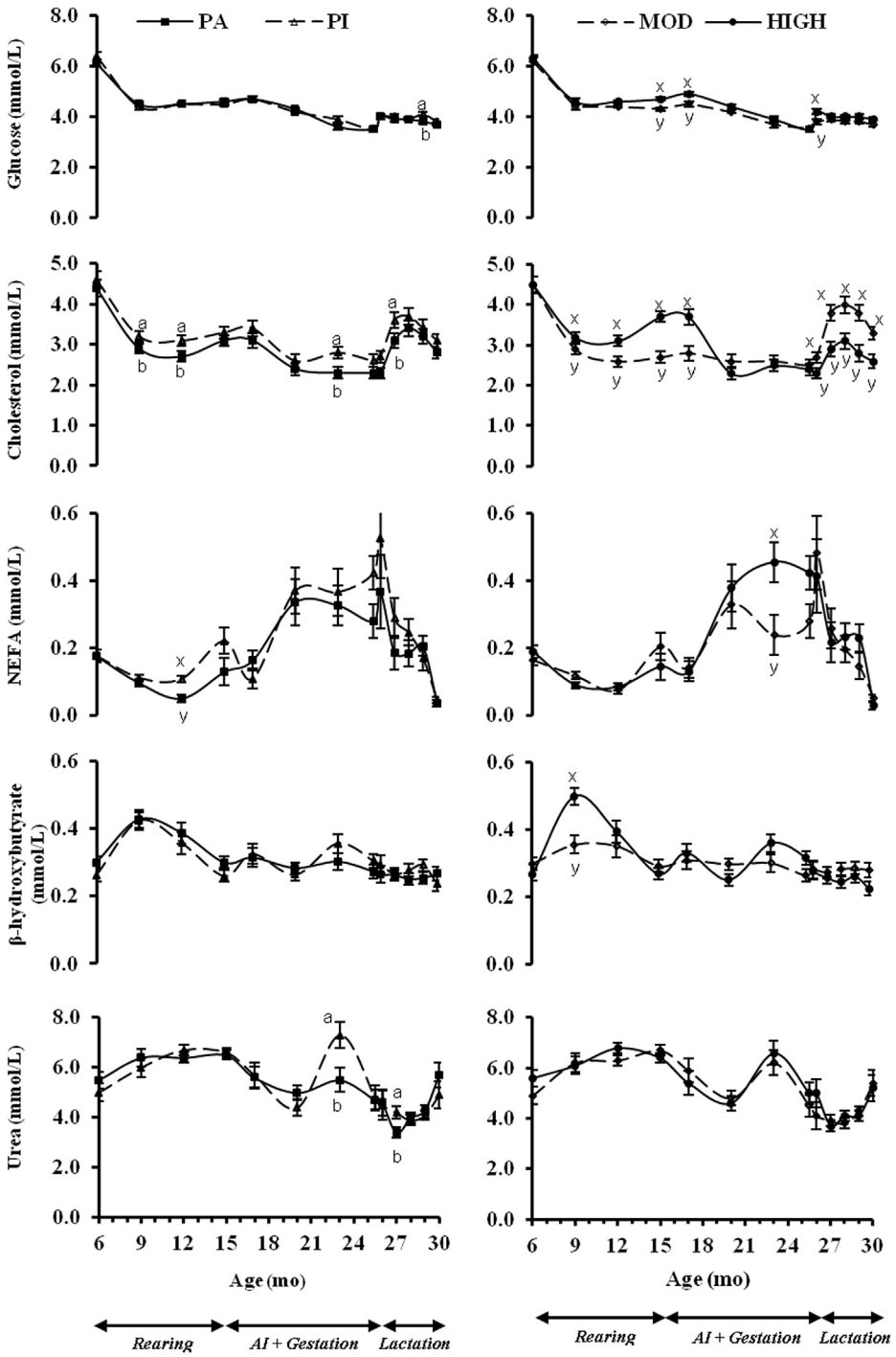

Fig. 4. Plasma concentrations of glucose, cholesterol, NEFA, β-hydroxybutyrate, and urea in beef heifers according to breed and feeding management applied in the postweaning period (6 to 15 mo). [a,b]LSMeans at a given age with different superscripts differ significantly among breeds ($P < 0.05$); [x,y]LSMeans at a given age with different superscripts differ significantly among feeding managements ($P < 0.05$). PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.

Circulating leptin increased through the postweaning phase and was fairly stable throughout the first gestation and lactation. Plasma leptin was unaffected by BREED or FEED and it was not related with any other metabolite or performance trait. Furthermore, no relationship was observed among different sampling times.

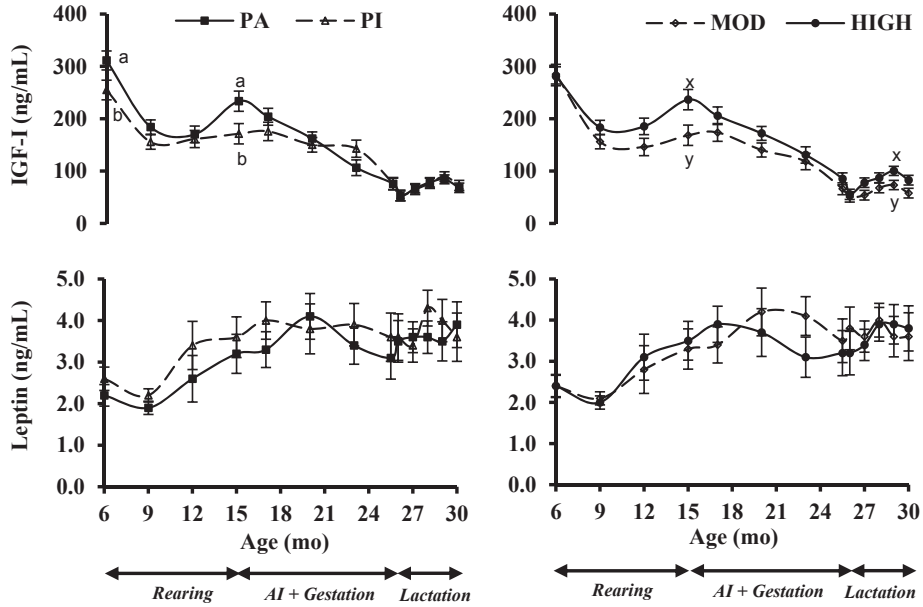

Fig. 5. Plasma concentrations of IGF-I and leptin in beef heifers according to breed and feeding management applied in the postweaning period (6 to 15 mo). [a,b]LSMeans at a given age with different superscripts differ significantly among breeds ($P < 0.05$); [x,y]LSMeans at a given age with different superscripts differ significantly among feeding managements ($P < 0.05$). PA, Parda de Montaña; PI, Pirenaica; HIGH, 0.8 kg/d target ADG; MOD, 0.6 kg/d target ADG.

4. Discussion

4.1. Growth performance

The target ADG during the postweaning phase was achieved in both FEED treatments, and consequently heifers from the HIGH treatment grew faster and at 15 mo they were heavier and tended to be fatter. The similar weight gains observed in heifers of both breeds throughout the study agree with previous results described in works both with heifers and growing bulls [20], likely due to their similar intake capacity [26] and feed conversion efficiency [28]. Considering their similar mature BW (580 kg [17]), at the time of conception, all heifers exceeded the minimum recommended BW to avoid future detriment to dam performance, that is, either 65% of mature BW [4] or the more restrictive 50%–55% recommendation [5,6]. After gestation on a common diet, heifer BW and BCS at calving were similar in all treatments and in accordance with those described in PA heifers having their first calving at 2 yr [8], but lighter than those of 2.5 yr-old PA primiparous [17]. Although the proportion of mature BW heifers at conception may have suggested excessive conditioning, their weight at calving was 81% of the expected mature BW in these genotypes, which roughly matched the 80% recommended by the NRC [7] for primiparous beef cows. Throughout lactation, all dams maintained their weight, but PA lost BCS and PI maintained it. This would confirm the lesser ability of lactating PA cattle to maintain BCS compared with PI cows, observed both under grazing [17] or confinement conditions [29]. This fact may be due to a different pattern of energy allocation, so that PA cows direct the energy mainly for milk production, whereas PI cows prioritize the accumulation or maintenance of body reserves [18].

Linear body measures are frequently used to complement weight as indicators of growth. Both breeds showed similar height at withers and heart girth throughout the experiment, indicating similar skeletal development. However, both traits were significantly greater at 15 mo in heifers from the HIGH than those from the MOD treatment, which confirms their different growth pattern. Height at withers at calving was 97% of that described by Álvarez-Rodríguez et al [30] (131 cm) for mature dry cows of the same breeds, and therefore, skeletal development at first calving could be considered as adequate for all groups. External pelvic area at 15 mo was smaller in PI heifers, which might reflect a later pelvic development, and in those of the MOD group, but these differences were offset during gestation and had no further effects.

4.2. Productive performance

All the heifers attained puberty at a similar BW, which confirms that puberty is reached at a critical BW around 55% of mature BW [31], irrespective of growth patterns. Freetly et al [31] suggested that this trait was a more robust predictor of age at puberty than absolute weight or age. This was also described by Grings et al [32] among beef heifers of 2 sire breeds differing in potential muscularity and raised on different dietary regimes. Puberty was reached before 300 d of age in 60% of the heifers, which can be considered as a precocious puberty [2], and this proportion was greater in the PA (77%) than in the PI heifers (42%). Weight at puberty did not differ between breeds but PA heifers attained puberty earlier, as observed previously [33], which could be ascribed to the ancient origin of PA in the Brown Swiss dual purpose breed because dairy breeds reach puberty earlier than beef breeds.

Some studies have indicated that diets promoting greater rates of gain early after weaning can increase the tendency to reach puberty at an earlier age, particularly when heifers are fed high-starch, gluconeogenic diets [2]. In the present study, puberty only tended to be achieved earlier in heifers from the HIGH than those from the MOD treatment, a trend that was confirmed at the individual level because rates of gain were negatively related to age at puberty. The fact that differences between treatments did not reach significance could be due to the limited number of animals, and also to the fact that all heifers had similar and high preweaning gains (1.039 ± 0.176 kg/d), which were greater than those observed in previous work with non–creep-fed calves of both breeds [17,26]. These high gains during lactation could have induced an earlier puberty, as suggested by Day and Nogueira [34]. Cardoso et al [35] reported that a favorable nutritional status between 4 and 6.5 mo of age induced functional changes in the neuroendocrine reproductive system that persisted after a period of feed intake restriction between 6.5 and 9 mo of age. Furthermore, Rodríguez-Sánchez et al [36] described a negative correlation between age at puberty and weight gains before weaning, but not with ADG after weaning. Conversely, Nepomuceno et al [37] found that enhanced nutrition during the postweaning period was an effective method to anticipate puberty, which was not influenced by preweaning calf supplementation. Nevertheless, all heifers involved in the experiment were pubertal early enough before the first AI. One of the main objectives of heifer replacement programs is to reach puberty 30 to 45 d before the breeding season [4], because the fertility rate increases after the pubertal estrous [38], which was achieved in the present study.

All primiparous cows calved at 26 mo, which is 10 mo earlier than usual in Spanish beef heifers [39]. Despite the fact that weight at calving complied with NRC recommendations, 36% of the primiparous cows needed assistance at calving. This rate was similar to an incidence of assistance of 38% described both for beef [40] and dairy heifers [24], and was not affected by any of the factors analyzed herein.

Regarding the offspring traits, calf weight at birth was greater in PA heifers, in agreement with previous results [17], but it was not affected by FEED, as described by Rodríguez-Sánchez et al [8]. Thereafter, offspring performance was not influenced by BREED or FEED, but calf growth during lactation was lower than that reported for the offspring of mature cows of both breeds [19]. Milk yield was unexpectedly low according to the objective of the diet, especially in PA dams, which had similar production to PI cows although it is usually lower in the latter [26]. In fact, all groups except PI-MOD had lower milk production than expected, perhaps as a response to the high gains reached by these groups before puberty, over 1 kg/d, while the PI-MOD gained 0.89 kg/d. Our results would confirm that prepubertal gains of around 0.8 kg/d can maximize milk yield, as described in dairy heifers [10], because greater prepubertal gains could increase deposition of mammary adipose tissue and impair parenchymal development of the mammary gland [13]. Furthermore, Dervishi et al [41] indicated that the lower milk yield of beef primiparous cows, which had been creep fed as calves, was associated with a different pattern of gene expression in the mammary gland, which suggested a compromised immune status during lactation.

4.3. Metabolic profiles

Some differences were observed in the present study in metabolic substrates associated with breed and feeding treatment in the rearing phase, but sampling date had a major effect in all cases, probably because of the strong short-term effect of current energy and/or protein intake. At the individual level, concentrations of the different metabolites were not related over time. Metabolic imprinting was only observed in the case of glucose and cholesterol, where feeding management in the juvenile period originated effects which persisted into lactation.

Glucose concentrations decreased after weaning because it is the main energy source for the lactating calf, but afterward there is a gradual shift in the sources of physiological fuel [42]. The greater values in the HIGH group were related to their greater concentrate intake in this phase, which resulted in a greater ruminal production of propionate [43], which once absorbed is the main source for glucose synthesis at the liver [44]. These differences were still evident in the first lactation, in agreement with other authors [15,45] who found that postweaning diets differing in concentrate content resulted in different glucose and insulin profiles, persisting into adulthood. The drop in glucose concentrations throughout gestation to the nadir registered 1 wk before calving could be caused by the reduced intake capacity in late gestation as fetus size increases [26].

Circulating cholesterol was affected by an interaction between feeding treatment and sampling time. In the rearing phase, the greater levels observed in the HIGH treatment were associated with their greater energy intake. By contrast, the greater concentration in the MOD treatment during lactation was mainly due to PI-MOD heifers, which also had the greatest milk yield, indicating a mobilization of fat reserves for milk secretion, as shown by Ruegg et al [46].

Plasma NEFA concentrations have been associated with the mobilization of fat tissue in replacement heifers fed different diets [47], but herein they did not differ among feeding treatments in any phase. In the rearing period, the greatest concentrations were observed in newly weaned heifers, probably because weaning is stressful and it increases the level of catecholamines, which stimulate lipolysis [48]. After breeding, values increased with advancing pregnancy and peaked at calving. In lactation, dam milk yield was correlated to plasma NEFA concentrations at calving, which implies that the fat mobilized was invested in milk secretion. The greater values observed in PI heifers throughout the study could reflect their greater reactivity to handling practices [49].

Plasma concentrations of ß-hydroxybutyrate depend both on energy balance and ruminal fermentation pattern because both internal lipolysis and absorption of butyric acid from the ruminal wall are major sources for ß-hydroxybutyrate [50]. In our study, the fermentation of a

diet with greater concentrate content induced a greater ruminal production of butyric acid in the HIGH feeding treatment [43], resulting in greater plasma ß-hydroxybutyrate during the rearing phase. The negative relationship observed between ß-hydroxybutyrate and NEFA concentrations could be explained by the fact that although both metabolites indicate short-term negative energy balance and adipose tissue catabolism, ß-hydroxybutyrate can also come from dietary sources [51].

Increased urea concentrations have been associated with a greater intake of dietary protein but also to the catabolism of body protein in periods of energy shortfall [14]. In the present study, circulating urea matched the pattern of estimated protein intake throughout the experiment, as both are positively correlated [52]. It increased throughout the rearing phase, as observed by Brickell et al [14] in dairy heifers. During lactation, plasma urea was less than 7 mmol/L, a level indicated by Butler [53] as the upper threshold to avoid impairing subsequent fertility in dairy cattle.

The positive relationship between urea concentration at 6 mo and cholesterol and the negative correlation with age at puberty confirms that puberty is hastened in heifers with better nutritional status at weaning [3]. Hence, levels of cholesterol and urea registered at 6 mo could be helpful indicators to estimate the capacity of the heifer to attain puberty early. As observed by Abeni et al [54], although large differences were not observed between dietary treatments for some metabolites, associations at the individual level reflect a strong within-animal relationship between metabolism and growth.

4.4. Endocrine profiles

Animal growth is controlled primarily by the somatotropic axis, formed by growth hormone, insulin, and IGF-I. Under diets formulated for high rates of gain (1.2 kg/d) through the first year of life, Govoni et al [55] observed that IGF-I increased particularly from 200 to 300 d of age in Hereford heifers and plateaued afterward. In the current experiment, however, the greatest values of IGF-I were observed at 6 mo, associated with high gains during lactation, and then they decreased with advancing age. Concentrations of IGF-I reached a nadir at calving, which could be associated with parturition stress [56], and they increased thereafter, as described in other works [57].

There were no differences between genotypes in their plasma IGF-I levels, as reported in previous work for suckling cows [29] and growing bulls [28] of the same breeds, which was associated with their similar growth potential. Heifers from the HIGH treatment showed greater values for IGF-I throughout the study, and at the individual level there was a strong correlation among concentrations in samples collected over time. This would confirm the theory of Reis et al [15], who reported that concentrate supplementation in early life had a long-term impact on the mRNA expression of hepatic IGF-I, but they could not find equivalent translation into circulating IGF-I concentrations.

The within-animal relationships observed between IGF-I, weight gains, and age at puberty have also been described in dairy heifers [14], confirming that IGF-I is an important metabolic mediator involved in the onset of puberty in beef cattle [58]. Similarly, the correlations of IGF-I with glucose and cholesterol reflect the bond of this growth factor with energy balance.

Circulating leptin increased through the postweaning phase, which was associated with fat deposition because leptin is a key metabolic signal synthesized by fat cells in white adipose tissue that communicates information about body energy reserves and nutritional status [59]. There were no differences between breeds, which agree with their similar BCS. Leptin was not influenced by FEED, and at the individual level, it was not related with gains or with age at puberty. Greater gains during juvenile development can induce adipose tissue accretion and enhance the synthesis and release of leptin, which signals the central nervous system of the availability of enough nutritional reserves to support the pubertal transition [60]. Therefore, the lack of effects observed here implies that nutritional status was adequate in both treatments. Similarly, Cooke et al [58] did not find that greater leptin concentrations hastened puberty attainment in beef heifers, and concluded that it served as a permissive signal that allows puberty to occur, but with a secondary role to that of IGF-I. The peripubertal rise in plasma leptin reported by Garcia et al [61] most likely reflects fat deposition but would not be a mandatory condition for the attainment of puberty, which can occur over a wide range of plasma leptin concentrations [62].

In conclusion, both postweaning growth rates (0.8 and 0.6 kg/d over a 9-mo rearing phase) allowed animals to surpass the threshold weights recommended for beef heifers both at conception (15 mo) and at calving (2 yr) in both breeds. Moreover, a moderate growth rate was sufficient to ensure metabolic and hormone profiles that were adequate for heifer development and performance until the first lactation, whereas no advantage was gained from a higher feeding level.

Acknowledgments

Appreciation is expressed to the staff of CITA Research Center and Drs C. Tamanini and N. Govoni from Università degli Studi di Bologna for technical support. Spanish Ministry of Economy and Competitiveness (INIA RTA 2010–057, RTA 2013–059 and RZP 2015–001), European Regional Development Fund and Research Group Funds of Government of Aragon (A11) funded this research. The first author received a grant from INIA-Government of Spain.

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