CSIRO PUBLISHING

Animal Production Science, 2020, **60**, 573–583
https://doi.org/10.1071/AN18254

Piglet birthweight and sex affect growth performance and fatty acid composition in fatty pigs

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Abstract. This study aimed to determine the effects of piglet birthweight (BIW) and sex, and within-litter BIW variation, on postnatal growth traits and meat quality in fatty breeds of pig. In total, 406 crossbred piglets (half male, half female) born to Iberian sows were studied during their postnatal development until slaughter. After birth, piglets were classified into four BIW categories: very low, low, medium and high. There was a negative effect of low BIW on growth patterns and fatty acid (FA) composition, but effects of litter size and within-litter BIW variation were not found. The very low BIW piglets underwent a period of significant catch-up growth ($P < 0.005$) relative to high BIW piglets during the early postnatal phase, but also showed a higher feed conversion rate and lower average daily weight gain ($P < 0.05$ for both measures) throughout the study period. BIW affected development during the entire productive life, and the sex effect increased with age. As a result, the period to reach market weight was longer in very low BIW piglets, by 43 days for females and 15 days for males, compared with their high BIW counterparts. BIW and sex also influenced amount of intramuscular fat, n-3 FA content and monounsaturated FA composition. The study indicates that BIW, modulated by sex, is a critical point for productive traits in fatty pigs. These results provide a basis for future strategies to enhance productive efficiency and meat quality of traditional swine breeds.

Additional keywords: carcass traits, Iberian pig, IUGR, lipids, meat quality.

Received 18 April 2018, accepted 24 June 2019, published online 17 January 2020

Introduction

The increasing demand for high-quality, dry-cured products from fatty breeds of pig has moved management practices toward the more intensive rearing regimes used for lean breeds. Current reproductive strategies for swine production aim to increase prolificacy. However, there is evidence in lean breeds that greater litter size (LS) generates higher within-litter variation in birthweight (BIW) (Quiniou *et al*. 2002; Quesnel *et al*. 2008) and a higher incidence of piglets with low and very low BIW (Foxcroft *et al*. 2006; Milligan *et al*. 2002). Available uterine space is decreased by increased prolificacy and leads to intra-uterine growth restriction (IUGR) processes, which may cause lower BIW in piglets (Wu *et al*. 2006). Intra-uterine growth restriction may be more severe in fatty breeds than in lean breeds because of the lower prolificacy and uterine capacity of the sows.

Lower BIW is associated with higher morbidity, different developmental patterns, and changes in body composition and homeostasis, due to prenatal programming through epigenetic changes (Gondret *et al*. 2005*b*, 2006; Gonzalez-Bulnes *et al*. 2016; Ji *et al*. 2017). Within-litter BIW variation (BIWV) may be associated with a high variability in carcass and meat quality in the same feedlot, which affects profitability and the production of dry-cured products (Andretta *et al*. 2016). Moreover, sex effects contribute to reducing feedlot homogeneity (Egea *et al*. 2016). Impaired postnatal growth patterns have been described for fatty breeds under experimental management (Gonzalez-Bulnes *et al*. 2012, 2014; Barbero *et al*. 2013). However, there is a lack of data under farm conditions, despite the high economic value of these breeds and their main differences from lean breeds (Nieto *et al*. 2012). Fatty pig breeds such as the Iberian breed produce well-recognised, dry-cured meat products of high quality (Lopez-Bote 1998). Homogeneity of growth patterns and meat quality within a feedlot are the primary goals in fatty pig production. However, fatty pigs show a lower weight homogeneity than lean breeds (Arévalo Mozos and Palomo Yagüe 2008; Soto *et al*. 2010).

The present study of fatty pigs under farm conditions aimed to determine the effects of BIW, within-litter BIWV and sex on postnatal development and carcass and meat quality at slaughter, including the fatty acid (FA) profile.

Materials and methods

Animals and diets

The study was performed according to the Spanish Policy for Animal Protection RD53/2013, which meets the European Union Directive (Directive 2010/63/EU revising Directive 86/609/EEC) on the protection of animals used for research. The experiment was specifically assessed and approved (report CEEA 2012/036) by the INIA Committee of Ethics in Animal Research. Animals were housed at a commercial farm, Ibéricos de Arauzo 2004 S.L. (Zorita de la Frontera, Salamanca, Spain).

In total, 406 crossbred piglets (~50% females and 50% males) were used in this study. They were born alive after insemination of 47 third-parity Iberian sows (Retinto strain) with cooled semen from Duroc boars (PIC (Genus plc), Stapeley, UK). The sows and offspring were managed in accordance with standard practices in commercial farms, including identification with electronic chips and housing indoors under controlled temperatures. Sows were allocated into groups for the first 101 days of pregnancy, and then placed in individual pens until the end of the suckling phase. Newborns were immediately sexed, measured, weighed and tagged. These piglets were allocated to mothers until weaning and then placed in collective pens. Males were surgically castrated within 2 days of birth. Sows and piglets were fed with standard, grain-based diets specific for Iberian pigs (diets are shown in Table S1, available as Supplementary Material to this paper), based on data from De Blas *et al*. (2013).

For experimental purposes, piglets were classified into four BIW categories: very low (VLBIW), low (LBIW), medium (MBIW) and high (HBIW). The classification was based on the mean and the standard deviation (s.d.) of the BIW of the study group of 406 piglets of 1.319 ± 0.313 kg (Blomberg *et al*. 2010; Vazquez-Gomez *et al*. 2016). The VLBIW group included piglets with a bodyweight below the mean minus 1 s.d. (BIW $\leq$0.99 kg); the LBIW group included piglets at the 30th percentile (after excluding VLBIW piglets, BIW 1.00–1.19 kg); the HBIW group included piglets from the 75th percentile (BIW $\geq$1.54 kg); and the MBIW group included piglets of BIW 1.20–1.50 kg.

At average age of 24 days (Day 24), 184 female and 175 male piglets were weaned. Of these, 132 females and 132 males (16 VLBIW, 24 LBIW, 55 MBIW and 37 HBIW pigs for each sex) were randomly selected and housed during the transition phase in groups of 12 piglets per pen, distributed by sex and BIW. During the growing–fattening phase (from Day 72 to slaughter), groups were randomly equalised to 120 males and 120 females (16 VLBIW, 24 LBIW, 44 MBIW and 36 HBIW pigs for each sex). Finally, 117 males and 115 females were slaughtered.

Evaluation of litter and piglet data at birth

Three litter-size categories were defined: small (total 3–6 piglets), medium (total 7–9 piglets), and large (total 10–13 piglets). The coefficient of variation (CV) and s.d. of BIW were calculated using the BIW of all piglets born alive for each litter.

Evaluation of growth pattern and fatness

Pigs were weighed from birth to slaughter at the following time points: birth, weaning (Day 24), at six points during postnatal growth (Days 71, 110, 150, 180, 215 and 240), and at slaughter, whenever they reached the minimum market weight (115 kg carcass weight; between Day 240 and Day 340). Bodyweight was determined individually at all these time points. On Day 340, the remaining pigs were sent to market regardless of their weight.

Average daily weight gain (ADWG) was calculated individually for the suckling phase, the transition phase (Days 25–71), five periods in the growing–fattening phase (Days 72–110, 111–150, 151–180, 181–215 and 216–240, with each period being labelled with the number of its last day), and the whole productive life. Feed conversion rate (FCR) for the five selected periods of the growing–fattening phase was calculated by pen, using the formula: daily feed intake block mean/ADWG of the period.

At birth and weaning, morphological measurements were recorded with a measuring tape. At weaning and at Days 110 and 215, backfat depth was determined at the level of the head of the last rib (P2 point) with an ultrasound machine (SonoSite, Bothell, WA, USA). At the slaughterhouse, the length of carcasses (from the posterior edge of the *symphysis pubica* to the anterior edge of the first rib) and the backfat thickness (at the last rib) were recorded. Carcass yield was calculated individually, using the formula: carcass weight/bodyweight at slaughter.

Tissue sample collection and drip-loss analysis

Samples of *longissimus dorsi*, the right lateral lobe of the liver and subcutaneous fat (SCF) at the measurement level were biobanked at −20°C until FA analysis. On the day of sampling, a sample of *longissimus dorsi* muscle was used for the drip-loss analysis (Calvo *et al*. 2016).

Evaluation of metabolic status

Metabolic status was assessed at slaughtering from blood plasma samples obtained by jugular puncture with 5 mL sterile heparin vacuum tubes (Vacutainer; BD, Franklin Lakes, NJ, USA). Plasma was separated and stored in vials at –20°C until assayed. Parameters for glucose (glucose and fructosamine) and lipid profiles (total cholesterol, high-density lipoprotein cholesterol, low-density lipoprotein cholesterol and triglycerides) were assessed with a clinical chemistry analyser (Crony Instruments, Rome). Plasma insulin concentrations in slaughter samples were also determined by using a Porcine ELISA kit (Mercodia, Uppsala, Sweden).

Evaluation of the fatty acid composition of diets

The one-step procedure proposed by Sukhija and Palmquist (1988) was used for the extraction and methylation of dietary FA. FA methyl esters were identified with a gas chromatograph (HP-6890; Hewlett Packard, Palo, Alto, CA, USA) with a flame ionisation detector and a capillary column (HP-Innowax: 30 m length, 0.32 mm i.d., 0.25 µm polyethylene glycol film thickness) (Lopez-Bote *et al*. 1997).

Evaluation of fat content and fatty acid composition of tissue samples

The lipids from intramuscular fat at the *longissimus dorsi* muscle (IMF) and liver fat were extracted as described by Segura and Lopez-Bote (2014). Total lipids in IMF and liver fat were separated into the main fractions: neutral lipids (NL) and polar lipids (PL) (Ruiz *et al*. 2004). SCF was separately analysed in outer and inner layers. Extracts were methylated (Segura *et al*. 2015*b*) and analysed using protocols developed at our laboratory (Lopez-Bote *et al*. 1997). Individual FA percentages for saturated, monounsaturated and polyunsaturated FA (SFA, MUFA and PUFA) were calculated. Total n-3, total n-6 FA, n-6/n-3 ratio and the unsaturated index were also calculated (Hulbert *et al*. 2007). The activity of stearoyl-CoA desaturase enzyme 1 (SCD-1) was estimated as C18:1/C18:0 and MUFA/SFA ratios (desaturation indices) (Hulver *et al*. 2005).

Statistical analyses

Data were analysed by using the GLM procedure in SAS version 9.4 (SAS Institute, Cary, NC, USA) with orthogonal contrasts (five contrasts). The first contrast was between sexes, the second between VLBIW pigs and other BIW groups, the third between VLBIW and LBIW pigs, the fourth between LBIW pigs and the sum of MBIW and HBIW pigs, and the fifth between MBIW and HBIW pigs. Changes over time in bodyweight and ADWG were assessed by a repeated-measures test with the Greenhouse–Geisser correction. BIW groups and sex were considered the main effects. Statistically significant interactions are presented. Sow was used as random effect in the birth and weaning analysis to account for the common maternal environment. Litter size was categorised into the three groups previously described and used as a random effect for birth data. For performance parameters, the respective age was used as a covariate. The Student's *t*-test was used to identify differences between sexes in each BIW group.

The Chi-squared test was used to assess the mortality data and the percentage of VLBIW piglets, as described above. Pearson's correlations were analysed using the PROC CORR procedure and regressions using the PROC REG procedure of SAS. The pig was the experimental unit for all variables studied except for the CV and s.d. of BIW and LS, where the sow was the unit, and for FCR data, with the pen. Tabulated results are expressed as mean ± root-mean-square error (RMSE), whereas graphical and text results are expressed as mean ± s.d. Statistical significance was accepted where $P \leq 0.05$.

Results

Litter size and morphometric data of newborns

The mean LS was 8.9 ± 2.6 piglets born per sow (total), or 8.6 ± 2.6 piglets born alive. VLBIW and LBIW piglets born alive represented 15.8% and 14% of the total piglets. All morphological measurements were affected by BIW ($P < 0.0001$; Table 1), and the only sex-related effect was a longer ($P < 0.005$) thoracic perimeter in female than in male piglets (23.9 ± 2.1 cm vs 23.4 ± 2.5 cm). There were no significant differences between sexes for mean BIW or incidence of smaller piglets (male vs female: 13.3% vs 18.3% for VLBIW and 15.3% vs 12.8% for LBIW).

Almost half of the litters (48.9%) were classified as high LS, 32% medium LS, and 19.1% low LS. Moreover, the greater the LS, the more ($P < 0.001$) LBIW piglets were found for both sexes. Therefore, the mean value of BIW was lowered ($P < 0.0001$) with higher prolificacy (1.51 ± 0.26 kg for low LS vs 1.41 ± 0.28 kg for medium LS vs 1.23 ± 0.31 kg for high LS). Consequently, mean BIW decreased by ~43 g per pig for each unit increase in the total number of piglets born ($P < 0.001$; Fig. 1). However, the relationship between LS and BIW was weak because of the high BIWV. The greater the LS, the more within-litter BIWV ($P < 0.005$; Table 2) and differences were found between LS categories by s.d. (0.18 ± 0.10 for low LS vs 0.25 ± 0.08 for

Table 1. Phenotypic parameters at birth and weaning for the piglets categorised into birthweight (BIW) groups

BIW groups: VL, very low; L, low; M, medium; H, high. Significant differences ($P < 0.05$) for a parameter between sexes within a BIW group are shown by different letters. Contrasts are: 2, VL vs (L + M + H); C3, V vs L; C4, L vs (M + H); C5: M vs H. RMSE, Root-mean-square error; ADWG, average daily weight gain

	n	VLBIW		LBIW		MBIW		HBIW		RMSE	*P*-values for contrast			
		Female	Male	Female	Male	Female	Male	Female	Male		2	3	4	5
Birth														
Bodyweight (kg)	406	0.8	0.8	1.1	1.1	1.4	1.4	1.7	1.7	0.1	<0.0001	<0.0001	<0.0001	<0.0001
Occipito-nasal length (cm)	406	11.9	11.6	12.3	12.4	12.7	12.6	13.0	13.1	0.6	<0.0001	<0.0001	<0.0001	<0.0001
Trunk length (cm)	406	19.6A	19.3B	21.5	21.3	22.8	22.8	24.5	24.4	1.4	<0.0001	<0.0001	<0.0001	<0.0001
Abdominal perimeter (cm)	406	15.7	15.1	17.1	17.3	18.5	18.5	20.3	20.0	1.3	<0.0001	<0.0001	<0.0001	<0.0001
Thoracic perimeter (cm)	406	20.2A	19.5B	22.5	22.2	24.4	24.1	26.1	25.9	1.2	<0.0001	<0.0001	<0.0001	<0.0001
Biparietal diam. (cm)	406	4.7	4.6	5.1	5.1	5.3	5.3	5.6	5.6	0.2	<0.0001	<0.0001	<0.0001	<0.0001
Max. thoracic diam. (cm)	406	5.6	5.5	6.4	6.4	6.9	6.8	7.4	7.4	0.5	<0.0001	<0.0001	<0.0001	<0.0001
Weaning														
Bodyweight (kg)	359	4.2	4.2	5.2	5.3	5.7	5.5	6.3	6.3	1.2	<0.0001	<0.0001	0.0003	<0.0001
Occipito-nasal length (cm)	359	15.2	15.1	16.0	15.8	16.3	16.3	16.5	16.6	1.0	<0.0001	0.0004	0.0007	0.03
Trunk length (cm)	359	35.1	34.8	38.8	38.5	40.2	39.5	42.3	41.3	4.0	<0.0001	<0.0001	0.0004	0.0002
Abdominal perimeter (cm)	359	30.5	30.4	33.2	33.1	34.3	33.9	36.2	35.1	3.8	<0.0001	0.0007	0.003	0.001
Thoracic perimeter (cm)	359	35.2	34.2	37.2	37.3	38.9	38.2	40.6	40.0	3.4	<0.0001	0.0004	<0.0001	0.0001
ADWG (g/day)	359	132.0	138.0	178.0	176.0	183.0	179.0	197.0	201.0	44.0	<0.0001	<0.0001	0.01	0.002

medium LS vs 0.27 ± 0.06 for high LS, $P < 0.01$). These data were reinforced by analysing BIWV by CV (12.1 ± 8.4% for low LS vs 18.4 ± 6.4% for medium LS vs 22.0 ± 4.7% for high LS, $P < 0.001$).

Effects of birthweight and sex on weaning traits

On average, 7.7 ± 0.7 piglets were weaned per sow, with no significant difference between sexes. Mortality was higher ($P < 0.0001$) in the VLBIW group (36%) than in heavier BIW groups (7%). Mean bodyweight at weaning was significantly correlated with BIW ($r = 0.50$, $P < 0.0001$; Table 2), and all morphological measurements were significantly different among BIW categories ($P < 0.05$ for all; Table 1). The lowest morphological measurements, weight and backfat depth (0.43 ± 0.11 cm vs 0.47 ± 0.12 cm, $P < 0.05$) were found in the VLBIW group, with significant differences relative to the other groups ($P < 0.001$ for all).

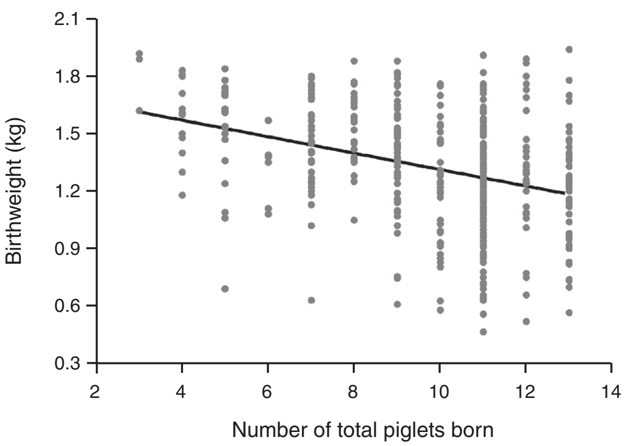

Fig. 1. Regression of the total number of piglets born per litter (PB) and birthweight (BIW). Equation: BIW = (1.74 ± 0.06) – (0.043 ± 0.006)PB; $R^2 = 0.11$, r.s.d. = 0.29, $P < 0.0001$.

Moreover, males showed greater backfat depth than females (0.48 ± 0.11 cm vs 0.44 ± 0.12 cm, $P < 0.01$).

Piglets in the VLBIW group also showed a lower ($P < 0.0001$) ADWG during the suckling phase (135 ± 38 g/day) than the other groups (mean 186 ± 47 g/day), and the LBIW group showed lower ($P < 0.05$) ADWG than piglets in groups MBIW and HBIW.

Effects of birthweight and sex on growing and fattening phases

At the end of the growth-transition phase (Day 71), VLBIW pigs continued showing lower ($P < 0.01$) ADWG (338 ± 76 g/day) than pigs from heavier BIW groups (381 ± 82 g/day). Moreover, LBIW pigs had lower ($P < 0.05$) weight and ADWG than the MBIW and HBIW pigs (Table 3).

At the beginning of the growing phase, at Day 110, LBIW pigs were heavier ($P < 0.01$) than VLBIW pigs (Table 3). Furthermore, HBIW and MBIW pigs showed lower ADWG and higher FCR than LBIW pigs ($P < 0.005$ for both; Table 3). There was a significant sex-related effect, with females showing higher weight and ADWG and lower FCR than males ($P < 0.01$ for both). Moreover, the changes in bodyweight and ADWG from birth to Day 240 were different among BIW groups and between sexes ($P < 0.0001$ for both).

At the following assessment, Day 150, VLBIW pigs remained lighter than the pigs in the other groups (54.0 ± 11.4 kg vs 58.7 ± 9.1 kg in the other groups, $P < 0.001$), mainly because of the lowest weight of VLBIW females at Day 150 ($P < 0.0001$; Fig. 2). At this age, the VLBIW category also showed lower ADWG and higher FCR than the other categories ($P < 0.0005$ for both; Table 3). At Day 180, VLBIW pigs continued to show lower ($P < 0.05$) weight and ADWG than pigs in the other groups, and FCR was lower ($P < 0.001$) with heavier BIW pigs. Regarding the sex effect, at Day 150, females had lower ADWG and higher FCR than males ($P < 0.0005$ for both). At Day 180, males showed higher ($P < 0.001$) weight and ADWG than females.

Table 2. Correlation coefficients for litter size, within-litter variation, weights and carcass traits of pigs

Asterisks indicate significant differences between birthweight groups: †, 0.1 > P > 0.05; *, $P < 0.05$; **, $P < 0.005$; ***, $P < 0.0001$. CV, coefficient of variation; s.d., standard deviation; BIW, birthweight; LS, litter size; WW, weaning weight; W, weight at specified age; DaM, days to market; CY, carcass yield; BD, backfat depth; IMF, intramuscular muscular fat

	LS	BIW	WW	Day 71W	Day 110W	Day 150W	Day 180W	Day 215W	Day 240W	DaM	CY	BD	IMF
CV of BIW	0.4**	–0.3**	0.0	0.0	0.1	–0.0	–0.1	–0.1	–0.1	0.1†	–0.1	–0.1	–0.1†
s.d. of BIW	0.3***	–0.0	0.1	–0.0	0.0	–0.0	–0.0	–0.0	–0.0	0.0	0.0	–0.1	–0.2*
LS		–0.3**	–0.1*	0.0	0.1	0.0	0.0	–0.1	–0.1	0.2*	0.1	0.1	0.0
BIW			0.5***	0.2**	0.1	0.1	0.1	0.1	0.2*	–0.3***	–0.2*	–0.1	–0.2**
WW				0.6***	0.5***	0.5***	0.4***	0.3***	0.3***	–0.3***	–0.2*	–0.2*	–0.2*
Day 71W					0.8***	0.8***	0.7***	0.6***	0.6***	–0.4***	–0.2**	–0.1	–0.1
Day 110W						0.8***	0.7***	0.6***	0.6***	–0.4***	–0.3**	–0.1	–0.1
Day 150W							0.9***	0.9***	0.8***	–0.6***	–0.3**	–0.1	0.0
Day 180W								0.9***	0.8***	–0.6***	–0.3**	0.0	0.0
Day 215W									0.9***	–0.7***	–0.3**	0.0	0.0
Day 240W										–0.8***	–0.3**	0.0	0.0
DaM											0.4**	0.0	0.0
CY												0.2**	0.1*
BD													0.2*

Table 3. Growth during growing and fattening phases and at marketing for the pigs categorised into birthweight (BIW) groups

BIW groups: VL, very low; L, low; M, medium; H, high. Significant differences ($P < 0.05$) for a parameter between sexes within a BIW group are shown by different letters. Contrasts are: 1, female vs male; 2, VL vs (L + M + H); 3, VL vs L; 4, L vs (M + H); 5, M vs H. †0.1 > P > 0.05; n.s., not significant. Int., BIW × sex interaction; RMSE, root-mean-square error; BW, body weight (kg); ADWG, average daily weight gain (g/day); DaM, days to market; FCR, feed conversion ratio (kg/kg). ADWG was calculated individually for the transition phase (Days 25–71 from birth), for five periods in the growing–fattening phase (Days 72–110, 111–150, 151–180, 181–215 and 216–240), with each period being named by its last day, and for the whole productive life

	n	VLBIW		LBIW		MBIW		HBIW		RMSE	*P*-value for contrasts					Int.
		Female	Male	Female	Male	Female	Male	Female	Male		1	2	3	4	5	
Day 71																
BW	258	20.9	21.3	24.2	23.6	23.6	25.7	24.4	25.2	3.75	n.s.	<0.0001	0.0007	0.001	0.02	<0.0001
ADWG	258	339.0	337.5	385.5	369.5	366.5	403.0	377.0	386.0	65.0	n.s.	<0.0001	0.007	0.04	n.s.	<0.0001
Day 110																
BW	240	36.7	34.3	40.7A	36.1B	35.6	35.8	37.5	37.8	5.25	0.008	0.002	0.008	n.s.	<0.0001	<0.0001
ADWG	240	437.5A	359.0B	459.5A	346.0B	323.0	285.5	350.5	357.0	94.0	<0.0001	†	n.s.	0.0002	0.0001	<0.0001
FCR	240	1.0A	1.3B	0.9A	1.4B	1.5	1.7	1.4	1.4	0.52	0.0007	†	n.s.	0.002	0.009	<0.0001
Day 150																
BW	238	49.9A	57.3B	60.6	61.0	57.1	58.6	58.8	58.4	7.46	n.s.	<0.0001	<0.0001	n.s.	0.01	0.0003
ADWG	238	378.5A	659.0B	556.5A	712.5B	614.5	651.5	608.5	591.0	129.5	<0.0001	<0.0001	0.0004	n.s.	n.s.	<0.0001
FCR	238	3.6A	2.0B	2.1	1.8	1.9	1.9	2.2	2.1	0.83	0.0002	<0.0001	0.0001	n.s.	n.s.	<0.0001
Day 180																
BW	237	69.4A	83.0B	84.8	86.6	80.2	84.4	81.7	83.1	9.58	0.0006	<0.0001	<0.0001	n.s.	n.s.	<0.0001
ADWG	237	557.0A	733.0B	691.0	732.0	658.5A	737.0B	652.0	706.5	107.0	<0.0001	0.02	0.01	n.s.	n.s.	<0.0001
FCR	237	5.0A	4.1B	3.8	4.1	4.0	3.9	3.1	3.2	0.72	n.s.	<0.0001	0.001	0.0004	<0.0001	<0.0001
Day 215																
BW	234	94.5A	114.2B	115.0	117.4	112.4	116.7	113.5	113.1	11.88	0.0006	<0.0001	<0.0001	n.s.	n.s.	<0.0001
ADWG	234	789.0A	891.0B	865.09	878.0	921.0	922.0	910.5	855.5	144.5	n.s.	0.02	n.s.	n.s.	†	0.01
FCR	234	4.4	4.2	3.8	4.2	3.7	3.9	3.8	4.2	0.83	n.s.	0.03	n.s.	n.s.	n.s.	0.04
Day 240																
BW	232	114.2A	134.1B	136.8	135.8	135.7	140.1	140.0	135.9	13.63	0.03	<0.0001	0.0004	n.s.	n.s.	<0.0001
ADWG	232	789.0	794.5	870.5A	736.5B	930.0	915.0	1058A	912.0B	195.0	0.02	0.02	n.s.	0.0001	n.s.	<0.0001
FCR	232	5.9	5.5	5.2	6.5	4.2	4.2	4.0	4.7	1.67	n.s.	†	n.s.	0.002	n.s.	<0.0001
Slaughter																
BW	232	143.3A	151.0B	153.1	151.9	153.4	153.9	153.0	155.1	7.53	0.02	<0.0001	0.003	n.s.	n.s.	n.s.
DaM	232	306.3A	284.7B	274.5	283.8	271.1	273.2	262.7	268.7	22.12	n.s.	<0.0001	0.004	0.009	†	n.s.
ADWG	232	464.5A	534.5B	562.5	541.5	568.0	566.5	587.5	579.5	61.0	n.s.	<0.0001	0.0009	0.04	n.s.	n.s.

During the fattening phase, the VLBIW group continued to have lower weight and ADWG at both Day 215 and Day 240, and greater FCR at Day 215, than the other groups ($P < 0.05$ for all; Table 3). At Day 240, the LBIW group also showed lower ADWG and higher FCR than HBIW and MBIW groups ($P < 0.005$ for both; Table 3), mainly because LBIW males showed higher FCR. Moreover, males showed higher weight and lower ADGW than females at Day 240.

At slaughter, assessment of ADWG for the overall period revealed that the VLBIW group had lower ($P < 0.001$) values than the other groups (508 ± 74 g/day vs 568 ± 63 g/day). Moreover, LBIW pigs showed lower ($P < 0.05$) total ADWG than HBIW pigs (Table 3). The average number of days to market (DaM) linearly decreased ($P < 0.05$) with BIW increase (Table 4, Fig. 3), so that DaM was negatively correlated with birth and postnatal weights (Table 2). Hence, the VLBIW group was the oldest to be slaughtered and the lightest at slaughter. Furthermore, VLBIW females were the lightest ($P < 0.0001$) individuals at slaughter (Table 3).

Regarding sex, in the simple linear regression between DaM and BIW, the intercepts and slopes of the relationship were different ($P < 0.05$; Table 4). DaM also accounted for 25% of the variation in weight at market, and the maximum point calculated was at Day 238, which means that beyond this time, weight at market decreased as DaM increased.

Effect of birthweight and sex on metabolic status

At slaughter, higher ($P < 0.05$) glucose concentrations were found in VLBIW pigs (127.3 ± 23.4 mg/dL) than in the other groups (mean value 107.6 ± 28.8 mg/dL), with a significant sex-related effect, VLBIW females showing the highest values (153.0 ± 14.1 mg/dL). On the other hand, plasma concentrations of insulin were highest in VLBIW males and lowest in VLBIW females (0.09 ± 0.05 µg/L vs 0.03 ± 0.00 µg/L; $P < 0.05$).

Effect of birthweight and sex on carcass traits and fatness

There were significant differences in fat accumulation between groups during postnatal development. The VLBIW group showed lower ($P < 0.05$) total backfat and outer layer depth than the other groups at Days 110 and 215 (Fig. 4). Moreover, the inner layer was thinner ($P < 0.005$) in the VLBIW group than in the other groups at Day 110. At Day 110, MBIW pigs had a thinner ($P < 0.05$) outer layer than HBIW pigs. The LBIW group showed thicker ($P < 0.05$) total backfat and inner layer than the heavier BIW groups at Day 215.

At Day 110, male pigs had a thicker ($P < 0.05$) inner layer than female pigs (0.33 ± 0.1 cm vs 0.30 ± 0.1 cm) but a thinner ($P < 0.05$) outer layer (0.52 ± 0.1 cm vs 0.56 ± 0.1 cm). At Day 215, males continued to have thicker ($P < 0.0001$) total backfat than females (2.36 ± 0.4 cm vs 2.13 ± 0.4 cm) and a thicker

(P < 0.0001) inner layer (1.12 ± 0.3 cm vs 0.94 ± 0.3 cm). Furthermore, VLBIW females had the lowest values at Day 215 (P < 0.05). Conversely, at slaughter, there were no significant differences in backfat depths of carcasses between groups or between sexes (Table 5).

Regarding carcass traits at market, carcass length was shorter (P < 0.05) in the VLBIW group than in the other groups (Table 5), with VLBIW females having the lowest carcass length and weight. Carcass yield was positively correlated with age at market (Table 2), and the LBIW group showed higher (P < 0.05) IMF than the heavier BIW groups. Sex effects were found for IMF and liver fat, which were higher (P < 0.05 for both) in males than in females (Table 5).

Effects of birthweight and sex on tissue fatty acid composition

There were significant effects of both BIW category and sex on the FA profile of lipids from IMF (Table S2), SCF (Table S3) and liver fat (Table S4). The composition of lipids in IMF was influenced by both BIW and sex. Specifically, in the PL fraction, the VLBIW group showed higher SFA and MUFA and lower PUFA concentrations than the other groups (P < 0.05 for all). The main differences in the NL fraction were found in

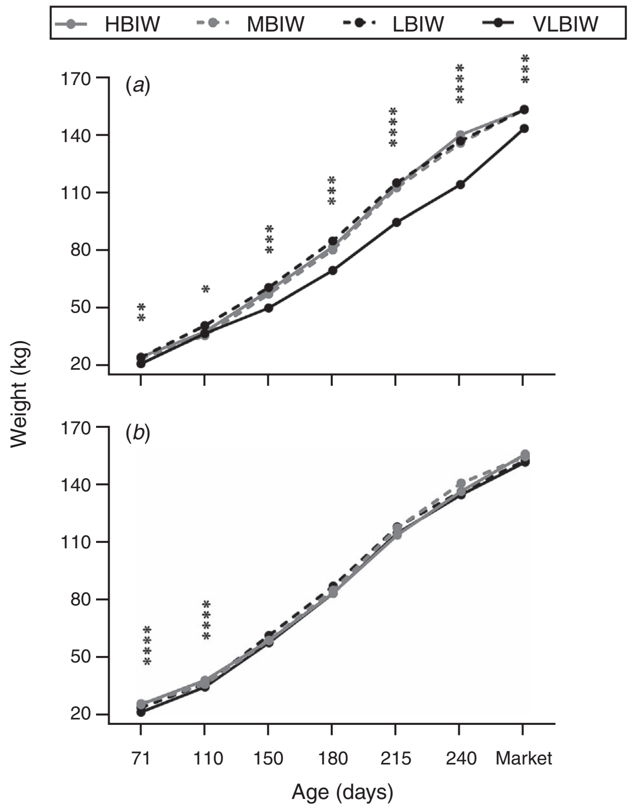

Fig. 2. Weight gain during growing and fattening phases until at-market in (*a*) females and (*b*) males distributed by birthweight (BIW) categories. Asterisks at a given sampling time indicate significant differences among BIW groups separated by sex: *, P < 0.05; **, P < 0.005; ***, P < 0.001; ****, P < 0.0001. BIW categories: H, high; M, medium; L, low; VL, very low.

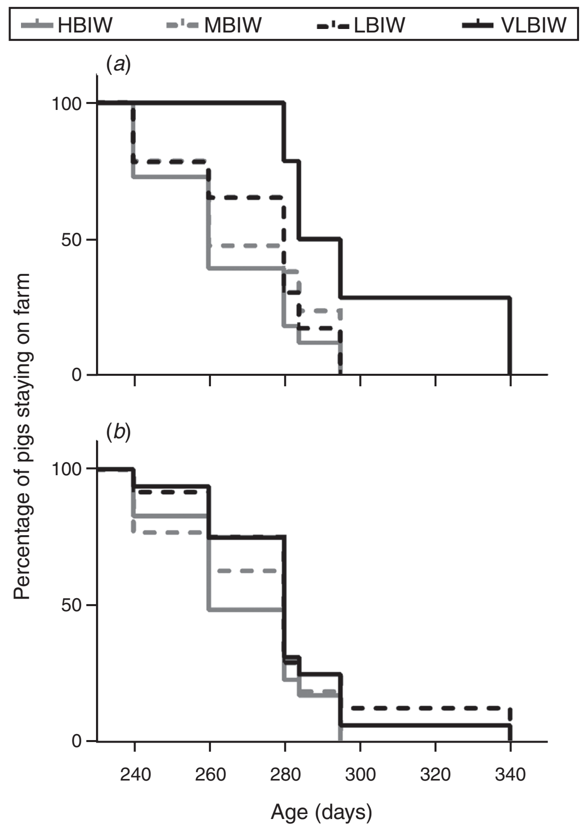

Fig. 3. Percentage of pigs staying on farm from the time of first pigs going to market, distributed by birthweight (BIW) categories of (*a*) females and (*b*) males. BIW categories: H, high; M, medium; L, low; VL, very low.

Table 4. Regression equations of days to market (DaM), birthweight (BIW, kg), average daily weight gain (ADWG, kg/day) and weight at slaughter (WM, kg)

According to sex in equations with both DaM and BIW, using Student's test, intercepts and slopes with different letters are different (P < 0.05)

	n	R^2	r.s.d.	P-value		
				Linear	Quadratic	Regression
DaM = (311.7 ± 7.4) – (27.6 ± 5.3)BIW	232	0.11	22.4	–	–	0.0001
ADWG = (1.25 ± 0.02) – (0.003 ± 0.00007)DaM	232	0.86	0.024	–	–	0.0001
WM = (55.2 ± 36.6) + (0.85 ± 0.002)DaM – (0.002 ± 0.0005)DaM^2	232	0.25	6.15	0.002	0.0003	0.0001
DaM (males) = (305.2b ± 9.6) – (22.2b ± 6.9)BIW	117	0.08	21.97	–	–	0.0001
DaM (females) = (320.5a ± 11.6) – (34.9a ± 8.3)BIW	115	0.14	23.02	–	–	0.0001

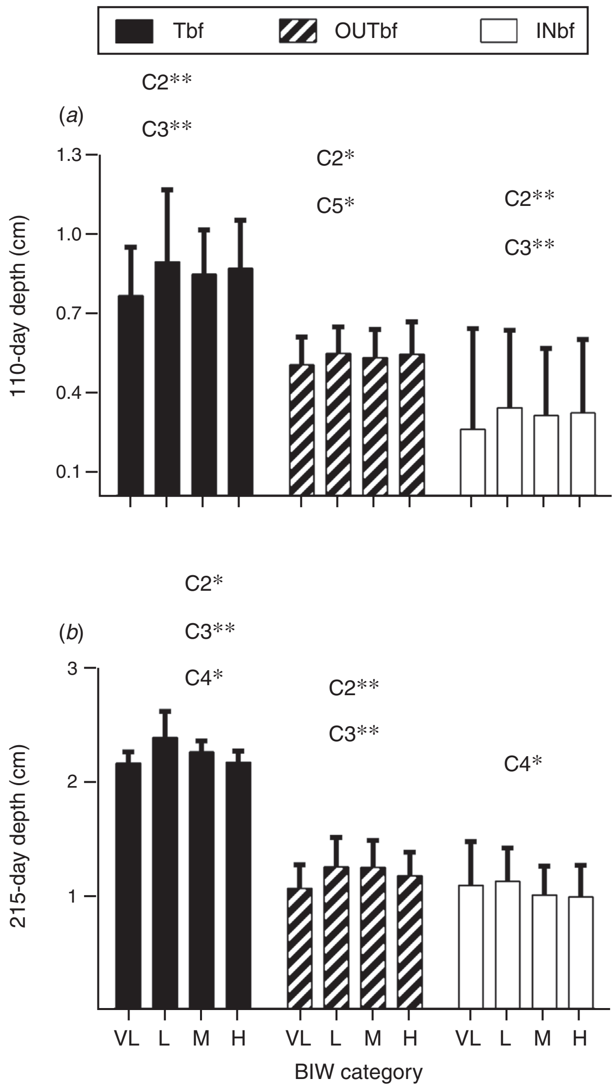

Fig. 4. Fatness during postnatal development. Mean values (± s.d.) of total backfat depth (Tbf, cm) and its outer (OUTbf) and inner (INbf) layers distributed by birthweight (BIW) categories at (*a*) 110 and (*b*) 215 days of age. BIW categories: VL, very low; L, low; M, medium; H, high. For each contrast (C), significant differences are indicated by asterisks: *, $P < 0.05$; **, $P < 0.01$. C2, VL vs (L + M + H); C3, VL vs L; C4, L vs (M + H); C5, M vs H.

heavier BIW groups. The MBIW group showed lower ($P < 0.01$) concentrations of C18:1 n-9 and MUFA and lower ($P < 0.05$) desaturation indices (C18:1/C18:0 and MUFA/SFA) than the HBIW group, but a higher ($P < 0.05$) value of SFA. Sex-related effects in both NL and PL fractions were found. Considering only the NL fraction, males had higher ($P < 0.05$) MUFA concentration and unsaturated index, but lower ($P < 0.05$) SFA value than females. In the PL fraction, males showed higher ($P < 0.05$) C18:1 n-9 content.

The assessment of the FA profile of SCF (Table S3) addressed mostly sex-related differences, except that, independent of sex, the HBIW group showed higher ($P < 0.05$) n-3 FA values than the MBIW group in the outer layer of SCF. A similar FA profile to that of the IMF NL fraction was found in both the outer and inner layers for males and females. Moreover, females also showed a higher ($P < 0.01$) $\sum$n-6/$\sum$n-3 ratio in the outer layer, with lower ($P < 0.005$) n-3 FA values at the inner layer.

Effects of BIW and sex were evident for liver fat (Table S4), with more significant differences between BIW groups in the NL fraction and more sex-related effects in the PL fraction. Assessment of the NL fraction showed that the VLBIW group had a higher SFA concentration and lower desaturation indices than the LBIW group ($P < 0.05$ for all). On the other hand, the LBIW group, compared with MBIW and HBIW groups, had higher ($P < 0.05$) MUFA concentrations and higher ($P < 0.001$) desaturation indices (C18:1/C18:0 and MUFA/SFA), and a lower ($P < 0.05$) SFA value. Sex-related effects were critical in the PL fraction, where C18:0 levels were higher ($P < 0.05$) for the VLBIW group than for the other groups; male and female VLBIW pigs were the most divergent in FA composition of the PL fraction, resulting in many significant global sex effects. Males showed higher C18:3 n-3 and MUFA concentrations and desaturation indices ($P < 0.05$ for all), but lower ($P < 0.005$) C18:0 and C18:2 n-6 values than females.

Discussion

The present study provides comprehensive evidence for the first time in a fatty breed of pig of the correlations between increases in LS and decreases in both BIW and within-litter BIW homogeneity. Subsequently, a low BIW penalised postnatal development and time to reach target weight, with carcass and meat quality decreasing within-feedlot homogeneity. These effects were also influenced by the sex of the offspring.

Table 5. Carcass and meat quality traits at marketing for the pigs categorised into birthweight (BIW) groups

BIW groups: VL, very low; L, low; M, medium; H, high. Significant differences ($P < 0.05$) for a parameter between sexes within a BIW group are shown by different letters. Contrasts are: 1, female vs male; 2, VL vs (L + M + H); 3, VL vs L; 4, L vs (M + H). †0.1 > P > 0.05; n.s., not significant. Int., BIW × sex interaction; RMSE, root-mean-square error

	n	VLBIW		LBIW		MBIW		HBIW		RMSE	*P*-value contrasts				Int.
		Female	Male	Female	Male	Female	Male	Female	Male		1	2	3	4	
Carcass weight (kg)	232	118.0	121.6	122.3	123.2	122.1	121.9	121.6	122.0	6.2	n.s.	n.s.	n.s.	n.s.	n.s.
Carcass yield (%)	232	79.0	79.6	79.9	79.6	79.3	79.3	78.6	78.8	2.2	n.s.	n.s.	n.s.	n.s.	n.s.
Carcass length (cm)	232	88.1	88.2	90.4	89.1	90.7	90.0	90.4	90.8	2.7	n.s.	0.002	0.03	n.s.	0.01
Backfat depth (cm)	232	5.3	5.3	5.2	5.2	5.2	5.2	5.0	5.1	0.7	n.s.	n.s.	n.s.	n.s.	n.s.
Muscular drip loss (%)	232	6.9	3.9B	6.0	5.6	5.2	5.8	5.5	5.4	2.9	n.s.	n.s.	n.s.	n.s.	n.s.
Intramuscular fat (%)	232	8.4	8.8	7.9A	9.5B	7.1	8.3	7.1	7.5	0.1	0.04	n.s.	n.s.	0.02	0.03
Liver fat (%)	232	5.5A	6.8B	6.6	6.5	6.1	6.2	5.7	5.9	0.0	0.02	n.s.	†	n.s.	n.s.

Crossbred pigs were used in this trial, and similar results during postnatal development could be expected in purebred Iberian pigs. However, more experiments are needed to confirm this hypothesis.

Effects of litter size on birthweight and homogeneity

Larger LS was related to lower mean BIW and a higher within-litter BIWV and incidence of VLBIW piglets. Such effects have been described for lean breeds (Milligan *et al*. 2002; Foxcroft *et al*. 2006; Quesnel *et al*. 2008). The last of those studies stated that LS and BIWV are also affected by genotype, parity, management and nutritional (epigenetic) factors. Our results support that LS exerts a more pronounced effect on genotypes with a lower prolificacy. In the present study, the decrease in BIW with increasing LS seems greater in the Iberian breed (43 g of BIW per additional piglet born) than in lean genotypes (33–35 g of BIW; Quesnel *et al*. 2008; Beaulieu *et al*. 2010).

Effects of offspring birthweight and sex on postnatal development and fatness

A lower BIW was related to higher mortality during the suckling phase, as described in lean breeds (Quiniou *et al*. 2002; Wolf *et al*. 2008), and to significant differences in postnatal development patterns, as also described for lean breeds (Quiniou *et al*. 2002; Wu *et al*. 2006; Beaulieu *et al*. 2010). Overall, mean bodyweight and ADWG were highly influenced by BIW during suckling and transition phases. Data were not balanced by litter of origin but the statistical analysis ruled out any deviation caused by this effect.

We emphasise that LBIW, but not VLBIW, increased ADWG compared with heavier littermates during the period between weaning and the end of the transition phase. However, both groups increased ADWG at Day 110, and the weight of all BIW categories was more-or-less similar. These effects were more evident in females. Such data support the existence of a catch-up growth effect during the beginning of the growing phase (mainly evidenced in females) to increase the survival prospects of lighter piglets (Gonzalez-Bulnes and Ovilo 2012). Previous studies of our research group (Ayuso *et al*. 2015*a*, 2016) have related this catch-up growth to higher gene expression of pathways involved in cell growth and proliferation or protein turnover, which underlines the resilience of traditional breeds such as Iberian pigs.

Females showed decreased growth levels in the following growing periods. This development was confirmed by FCR, especially in VLBIW females, which did not maintain the expected growth rate during the growing or fattening phases. Hence, VLBIW females, despite catch-up growth at early postnatal stages, showed the lowest market weight and therefore the longest DaM value.

Overall, these results indicate that individuals with lower BIW do not compensate their low BIW during postnatal growth and are less efficient (higher FCR) than heavier littermates, which is similar to previous findings in lean breeds (Gondret *et al*. 2005*b*; Rehfeldt and Kuhn 2006; Bérard *et al*. 2008; Beaulieu *et al*. 2010). Moreover, a higher BIW was related to higher overall ADGW during the study period. Therefore, increases in the incidence of VLBIW and LBIW piglets enlarge the DaM period and raise production costs. Consequently, as the number of extra days needed to reach target market weight increases, the production costs relative to heavier BIW pigs also increases. In a lean genotype, Beaulieu *et al*. (2010) found a 10-day difference in reaching DaM between the lightest and heaviest BIW groups. In our study, the difference was larger in fatty pigs, being 15 days for males and 43 for females.

Effect of offspring birthweight and sex on back fat deposition and metabolism

The differential effects of BIW and sex on postnatal development were also observed in backfat deposition. Pigs from the VLBIW group showed lower backfat depth than pigs in the other BIW groups in the earlier life-periods; however, both VLBIW and LBIW pigs showed greater backfat depth at older ages (except for VLBIW females). This increase was particularly evident in the inner fat layer, which has more metabolic activity (Hausman and Thomas 1984). These results coincide with data from commercial breeds (Gondret *et al*. 2005*a*; Attig *et al*. 2008; Schinckel *et al*. 2010) and support the fact that lighter pigs have a higher tendency to accumulate fat, based on data supporting the hypothesis of prenatal programming.

Differences in glucose metabolism related to BIW were found at the end of the study. The VLBIW pigs showed higher glucose concentrations, which may be linked to an early prodrome of insulin resistance, modulated by sex, because VLBIW females had a low secretion of insulin but VLBIW males had the highest secretion of insulin (concomitant with a higher backfat depth).

Because the liver is the largest visceral organ, its status in individuals might affect physiological processes. Differences observed in backfat accumulation might be associated with the higher MUFA and desaturation indices of the lowest BIW groups, except VLBIW females, compared with the heaviest BIW groups. High SCD-1 activity has been related to metabolic disorders such as obesity and insulin resistance (Hulver *et al*. 2005; Poudyal and Brown 2011), although the LBIW group showed a regular at-market value of insulin. However, this higher activity of SCD-1, which plays a central role in *de novo* lipogenesis, might be linked to the beginning of an increase in liver fat storage. This is supported by the higher C16:1 content of LBIW pigs, this FA being considered an adiposity marker (Paillard *et al*. 2008). Other studies have found that decreased SCD-1 activity promotes lipid oxidation in lipid storage (Dobrzyn *et al*. 2004, 2005). This lower activity could be related to the lowest ratios of desaturation indices in VLBIW females and the lowest liver fat content. Further experiments are warranted to increase understanding of fat metabolism in LBIW pigs.

Effect of offspring birthweight and sex on carcass and meat quality at slaughter

The results for carcass traits revealed shorter carcass length for VLBIW pigs than for pigs in the other groups, which would be linked to poorer development in the growing–fattening phase. In fact, VLBIW females had the lowest carcass length and weight, which is consistent with their poorer postnatal development. Such an effect is well known in lean breeds, with carcasses from lighter BIW pigs having a lower weight of primary cuts, lower meat content and poorer meat quality (Rekiel *et al*. 2014).

Despite previous findings, no differences were found in backfat depth between BIW and sex categories at slaughter. This could be associated with the greater adipogenic capacity of Iberian pigs than of lean breeds (Nieto *et al*. 2012). Conversely, IMF content was higher in the lowest BIW groups and in males than in the heaviest BIW groups and in females, respectively. These data coincide with earlier studies in both lean and fatty breeds (Rehfeldt *et al*. 2008; Egea *et al*. 2016; Martinez-Macipe *et al*. 2016). Possible causes for IMF deposition in LBIW pigs may be related to a process of hyperplasia (increases in adipose cell number) during prenatal stages (Hausman *et al*. 2014).

Fatty acids in tissues are mostly distributed in PL and NL fractions, predominantly in the NL fraction (Wood *et al*. 2008). In the IMF, the NL fraction represents 70% of total FA, and is an estimator of total IMF FA (Ayuso *et al*. 2015b). Moreover, the membrane composition (PL) is more stable than the composition of storage lipids (NL) because of its functional properties (Sampels *et al*. 2011).

The loin is one of the most important carcass cuts in pork production and has a high economic value in the Iberian pig. Alvarenga *et al*. (2014) did not detect any effect of BIW on IMF composition when comparing light and heavy BIW pigs, but in our study, there were significant differences in the NL fraction of IMF between these groups. In the IMF NL fraction, the main differences were between MBIW and HBIW pigs. The HBIW group showed higher C18:1 n-9, MUFA, desaturation indices and unsaturated index than the MBIW group. In the Iberian pig, C18:1 n-9 has been used as an indicator of quality meat products, and high levels in backfat or meat pieces are linked to relevant traits of meat product quality, highly valued by consumers because of the association with the production of volatile fatty acids derived from oleic acid (Barea *et al*. 2013). Moreover, an increase in PUFA and MUFA meat levels is a priority because it enhances consumer acceptance owing to possible health and sensorial benefits (Laitinen *et al*. 2006; Jakobsen *et al*. 2009). In the PL fraction of IMF, the VLBIW group showed lower PUFA values and unsaturated index than heavier BIW groups.

A sex-related effect on the FA profile has been reported in many studies (Segura *et al*. 2015*a*; Daza *et al*. 2016; Egea *et al*. 2016). Differences between males and females were similar in SCF, IMF and the PL fraction of the liver. Overall, males had higher MUFA, but lower SFA and $\sum$n-6/$\sum$n-3 ratio than females. This is interesting in view of the human dietary recommendations of a $\sum$n-6/$\sum$n-3 ratio of 1 : 4 and higher MUFA values, as described above (Simopoulos 2002, 2010). From the present study, the FA profile is better in males than in females regarding meat quality.

Conclusions

This study clearly supports, for fatty breeds, that strong increases in LS are related to higher within-litter BIWV and a higher incidence of lighter BIW piglets. Our results also support the adverse effects of low BIW on postnatal growth traits and meat quality in fatty pigs. Pigs with lower BIW, despite catch-up growth processes, have lower ADWG and higher FCR during the growing and fattening phases, which increases daily feeding costs and induces a longer period to reach target weight. VLBIW females and males took 43 and 15 days longer than respective HBIW females and males to reach the market value. This situation, of course, increases production costs and reduces benefits.

Regarding carcass and meat traits, lighter BIW piglets presented poorer quality in carcass measurements, IMF values and FA profiles. Moreover, the HBIW group showed higher meat quality than MBIW pigs in the IMF FA profile. All of these effects were accentuated by sex, with females showing less growth potential than males during the growing phase and, at market, producing meat with lower organoleptic and health quality attributes.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

We thank Antonio Palomo for the diet data, the staff of Ibéricos de Arauzo S.L. for their help with the animals and I. Martín de la Torre and M. L. Pérez-Solana for their technical support with FA and metabolic analyses, respectively. We also thank Anayansi Ramírez, César Ocasio and Bosco Vidovik for their help. This research was supported by the Ministry of Economy and competitiveness (project AGL2013-48121-C3-R and AGL2016-79321-C2-2-R), co-funded by FEDER. More funds were obtained from MEDGAN-REDLAB (project S2013/ABI-2913) and CAM, co-funded by FEDER. MVG and CGC are supported by the FPU and FPI National Program of the Spanish Government, respectively (MVG: FPU014/01285; CGC: BES-2014-070464).

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Handling editor: Kate Plush